Fall 2006

Understanding changes in aboveground biomass and height with elevation at Hubbard Brook Experimental Forest

Mariya Schilz
University of New Hampshire, Durham

UNDERSTANDING CHANGES IN ABOVEGROUND BIOMASS AND HEIGHT WITH ELEVATION AT HUBBARD BROOK EXPERIMENTAL FOREST

BY

MARIYA SCHILZ

BA, University of California, San Diego, 2000

THESIS

Submitted to the University of New Hampshire

in Partial Fulfillment of

the Requirements of the Degree of

Master of Science

in

Natural Resources

September 2006

This thesis has been examined and approved.

Thesis Director, Dr. George C. Hurtt
Assistant Professor of Natural Resources and Earth, Oceans, and Space

Dr. Mary E. Martin
Research Assistant Professor of Natural Resources and Earth, Oceans, and Space

Dr. Barrett N. Rock
Professor of Natural Resources and Earth, Oceans, and Space

Dr. G. James Collatz
Physical Scientist
Biospheric Sciences Branch, NASA's Goddard Space Flight Center

Dr. N. Michele Holbrook
Professor of Biology and Charles Bullard Professor of Forestry
Harvard University

Dr. Ralph O. Dubayah
Professor of Geography
University of Maryland, College Park

July 27, 2006
Date

ACKNOWLEDGEMENTS

First of all I would like to extend my deepest gratitude to my graduate committee, Drs. George Hurtt, Mary Martin, Barry Rock, Jim Collatz, Ralph Dubayah, and Missy Holbrook. They have shared with me much of their time and insights.

Working within the Complex Systems Research Center at the Institute for the study of Earth, Oceans and Space at UNH has been an amazing experience. I have received endless support and assistance from Dr. Scott Ollinger, Matt Fearon, Steve Boles, and Michael Routhier. Thanks to Lucie Plourde for all her help processing the AVIRIS data. Tom Lee kindly allowed me the use of his lab and dendrochronometer.

Many thanks to Paul Schwarz for providing an incredible amount of data and responding to our questions with thought and generosity. Tom Siccama, Ellen Denny, Andrew Richardson, and Tim Fahey gave me much insight into field work and field data at Hubbard Brook and in the White Mountains of New Hampshire.

I am grateful for financial support from NASA's Research and Discover Fellowship Program. NASA scientists Drs. Jeff Morisette, Feng Gao, Greg Ederer, Robert Wolfe, and Jeff Pedelty were extremely helpful and provided me with phenology metrics from MODIS data.

I would also like to thank the UNH Graduate School for travel support.

Last but not least, I would like to thank my family and friends for their love and support.

TABLE OF CONTENTS

ACKNOWLEDGEMENTS.....iii

LIST OF FIGURES.....vi

ABSTRACT.....ix

CHAPTER PAGE

I. INTRODUCTION.....1

Site Description.....7

II. ANALYSES OF FACTORS EXPLAINING AGB AND HEIGHT DECLINE WITH ELEVATION.....9

Ecosystem Structure.....10

Growth and Mortality.....13

Sampling Design.....16

Collection and Analysis of Tree Cores.....17

Direct and Indirect Environmental Effects.....20

Direct Environmental Effects.....20

Indirect Environmental Effects.....25

III. DISCUSSION.....27

LIST OF REFERENCES.....52

APPENDICES.....58

APPENDIX A: Hydraulics and Height Limitation.....59

APPENDIX B: Isotope Analysis of Drought Stress.....61

APPENDIX C: Applicability of Hyperspectral Remote Sensing.....64

LIST OF FIGURES

Figure 1a: Plot level AGB versus elevation. Data courtesy Paul Schwarz. T-test p-value<0.0001, N=372. **1b**: LiDar height versus elevation. Data courtesy Ralph Dubayah. T-test p-value<0.0001, N=2959. **1c**: Plot level tree height, Schwarz laser range finder measurements. T-test p-value<0.0001, N=1075.

Figure 2: Diagram of levels of understanding changes in AGB and height with elevation at Hubbard Brook. Different tiers for our analysis of fine scale heterogeneity in forest carbon stocks.

Figure 3: Map of Hubbard Brook and Schwarz Valley Wide plots.

Figure 4: Plot average DBH versus elevation. T-test p-value<0.0001. N = 372.

Figure 5: Number of individual trees in each plot versus elevation. T-test p-value<0.0001. N = 372.

Figure 6: Frequency of coniferous and deciduous species by elevation class. Each elevation band value calculated by dividing AGB of each species type by total AGB.

Figure 7: Plot level AGB derived from same application of Yellow Birch allometry to each individual tree's DBH. T-test p-value<0.0001, N=372.

Figure 8a: Rate net AGB accumulation versus elevation. This plot demonstrates the relationship between our growth term and elevation. The rate of net growth decreases by 26% between 300 and 900 m in elevation. This growth term is derived by dividing the average of AGB per plot by each age. T-test p-value = 0.0013, N=452. **8b**: RI Growth: tree increment core derived plot level 1 year (averaged over 5 years) change in AGB with elevation. This growth measurement shows a decrease of 36% between 300 and 900 m in elevation.T-test p-value<0.0001, N=382. **8c**: AGB accumulation versus net growth as derived by radial increment. Intercept constrained to 0. T-test p-value<0.0001. N = 329.

Figure 9a: Minimum age versus elevation, Schwarz field data collected from each of the 431 Valley-wide plots. The relationship between average minimum age and elevation decreases by 25.44 years between 300 and 900 m elevation. T-test p-value=0.0121, N=452. **9b**: 2005 re-sample, plot minimum age versus elevation. T-test p-value=0.0682, N=117. Each point represents the minimum age of a single tree within one of the Valley-wide plots resampled during the 2005 summer. This plot substantiates the Schwarz age and elevation trend with an average plot age decline of 26.04 years between 300 m and 900 m elevation.

Figure 10: Relative importance of changes in net growth and mortality rates on change in AGB between 300 and 900 m elevation at Hubbard Brook.

Figure 11a: Hubbard Brook meteorological data average precipitation versus elevation. T-test p-value<0.0001, N=24. **11b**: Hubbard Brook meteorological data average minimum temperature versus elevation. T-test p-value=0.0007, N=8. **11c**: Hubbard Brook meteorological data average annual temperature versus elevation. T-test p-value=0.0014, N=8.

Figure 12a: Processed AVIRIS scene of Hubbard Brook and Valley plots. **12b**: AVIRIS image plot value N versus elevation. T-test p-value<0.0001, N=430. **12c**: Field Nitrogen versus elevation. T-test p-value=0.1173, N=26.

Figure 13a: Arcview image of MODIS derived growing season length overlaid with DEM elevation contours. White grid cells are no data. **13b:** 2002 MODIS derived growing season length versus elevation. MODIS growing season length shows the same 16% decline between 300 and 900 m elevation. T-test p-value<0.0001, N=101. **13c:** 1999 phenology data collected from 9 field sites at Hubbard Brook. Yellow birch, American beech, and Sugar maple trees monitored for leaf-on in the spring and leaf-off in the fall. Growing season length shows an average decrease of 16% between 300 and 900 m elevation. T-test p-value<0.0001, N=27.

Figure 14a: Schwarz field data average plot soil depth versus elevation. T-test p-value<0.0001, N=432. **14b**: Hubbard Brook GIS data on soil type, grouped by elevation. At each elevational band (Low, Mid, and High), the area of each soil type is divided by the total area.

Figure 15a: LiDar analyses of canopy height versus aspect at all elevations. T-test p-value<0.0001, N=2958. **15b:** LiDar analyses of canopy height versus aspect at high elevations (750-850 m). T-test p-value<0.0001, N=403. **15c:** LiDar analyses of canopy height versus aspect at mid elevations (550-650 m). T-test p-value<0.0001, N=827. **15d:** LiDar analyses of canopy height versus aspect at low elevations (350-450 m). T-test p-value=0.1943, N=403.

Figure 16: Percent change between 300 and 900 m elevation. First three bars represent the trends of interest: AGB, field measured height, and LiDar measured height. DBH and Number of Individuals (per plot) represent 'Ecosystem Structure' hypotheses. RI Growth, Net Growth, and Age are within our category of 'Growth and Mortality'. Average Temperature, Average Minimum Temperature, Average Precipitation, AVIRIS N, Field GSL (Growing Season Length), and MODIS GSL are all within our category of 'Direct Environmental Factors', and Soil Depth and Slope are within the 'Indirect Environmental Factors' category.

Figure 17: Regressions of environmental factors by AGB.

Figure 18: Radial increment growth estimate versus AVIRIS derived N concentration (% foliar weight). T-test p-value<0.0001, N=329.

ABSTRACT

EVALUATING CHANGES IN ABOVEGROUND BIOMASS AND HEIGHT WITH ELEVATION AT HUBBARD BROOK EXPERIMENTAL FOREST

by

Mariya Schilz

University of New Hampshire, September 2006

A better understanding of carbon stocks and fluxes is a priority of many national and international agencies, including NASA, NACP, IPCC, and IGBP. (Asrar et al. 2001, IGBP Annual Report, 2003, IPCC Third Assessment Report: Climate Change 2001). Patterns of carbon stocks and fluxes on the land surface are important for studies of the carbon cycle, climate change, and terrestrial ecology. One source of heterogeneity is associated with elevation. In systems around the world, patterns in carbon stocks, fluxes, and the factors that underlie them have well documented relationships with elevation (Korner 1999, Schwarz et al. 2003, Waide et al. 1998, Whittaker and Neiring 1975, Weaver 1990). One system well suited to study these patterns and their causes is Hubbard Brook Experimental Forest (HBEF), where field data and remote sensing data demonstrate that forests exhibit decreased height and aboveground biomass (AGB) with elevation. Here, we address the relative importance of various factors that contribute to these patterns. Our analyses are organized into the following four levels of hypotheses: changes in tree ecosystem structure, changes in rates of growth and mortality, direct environmental factors, and indirect environmental factors. We address these hypotheses

through statistical analysis of HBEF field and remote sensing data. We find that changes in rates of net growth are responsible for approximately 60% of the change in average AGB between 300 and 900 meters (m) while changes in rates of plot age-resetting mortality are responsible for the remaining 40%. These changes are associated with an increase in stem density, decrease in tree size, decrease in average temperature, shorter growing season length, decreased foliar N, and decreased soil depth with elevation. Results from this study will improve the understanding of carbon stocks and fluxes and enable better estimates of carbon sequestration in terrestrial ecosystems.

CHAPTER I

INTRODUCTION

Understanding patterns of carbon stocks and fluxes on the land surface is important for studies of terrestrial ecology, the carbon cycle, and climate change and is an increasingly high priority for environmental policymakers and scientists (Asrar et al. 2001, IGBP Annual Report 2003, IPCC Third Assessment Report: Climate Change 2001). This need is especially relevant in areas of mountainous terrain, where methodological challenges limit the usefulness of atmospheric methods such as eddy covariance (S. Ollinger, *personal communication*), and fine scale patterns of abiotic heterogeneity have a strong cumulative effect on the predictions of carbon stocks and fluxes. From the general example of tropical forests to alpine treelines, to specific examples at mountainous sites worldwide, the trend of biomass decline with increased elevation is well documented (Korner 1999, Schwarz et al. 2003, Waide et al. 1998, Whittaker and Neiring 1975). Work in the Central Himalaya documents both a biomass decline and a species shift at higher elevations (Singh et al. 1994). A 600 m gradient in the Luquillo Mountains of Puerto Rico demonstrates increases in stem density, basal area, and soil organic matter,

and decreases in canopy height, forest biomass, and species richness at higher elevation sites (Weaver 1990). On Mount Kinabalu in Borneo, two different substrate types both showed decline in aboveground net primary productivity (ANPP) with increases in elevation (Kitayama and Aiba 2002). In Northeastern U.S. forests, changes in foliar nutrients occur along an elevational gradient (Richardson 2004) as well as hyperspectral evidence of physiological changes with elevation (Goetz at al. 1983). (Refer to Appendix I and II).

One major set of hypotheses for decreased AGB and height at elevation are related to plant growth and the factors that influence it. Because so many factors are involved in growth limitation, and because so many environmental factors change with elevation, there may be numerous hypotheses on which factors play the largest role in plant growth: changes in temperature, precipitation, soils, or increased exposure to wind and storms. High elevation forests exist under extreme growing conditions which can include low fertility soils, lower water availability, harsh climate, higher pollution exposures (Weathers et al. 2000), and shorter growing seasons. Even when grown in a garden, Norway spruce seedling height and dry mass declines with altitude of seed origin. Since these responses are similar to those of seedlings from origins along a latitudinal gradient, they are assumed to be climate driven (Oleksyn et al. 1998). Korner (1999) and Oleksyn et al. (2002) propose that nutrient accumulation and retention are processes that adjust to environmental changes and increase metabolic capabilities in nutrient limited systems. Barrick and Schoettle (1996) hypothesized that treelines are determined by nutrient availability. Richardson (2004) utilized elevational gradients to evaluate plant responses

to environmental heterogeneity. He noted the lack of data on the limits for survival on trees at high elevation.

One extreme example of the impacts of elevation and associated reduced growth rates on forest dynamics is the krummholz zone which is characterized by trees exhibiting stunted growth as caused by the wind (Wardle 1968). Increased exposure to colder temperatures at higher elevations may have a limiting effect on nutrient availability and plant uptake of nutrients. This nutrient limitation may be related to the temperature dependence of microbial organisms and plant metabolic activity (Richardson 2004). Richardson (2004) looked specifically at foliar chemistry of balsam fir and red spruce along a canopy light and elevational gradient in the northeast U.S. His transect included the bottom edge of the spruce-fir forest (low elevation), the tree line where at transition from forest to krummholz (mid elevation), and the highest patches of krummholz (high elevation). He noted a higher average concentration of macronutrients (N, P, K, Ca, Mg) at lower elevation sites. Richardson found that K concentrations decreased 20% from low to high elevation sites. Decreasing levels of foliar lignin and cellulose were found with increases in elevation. Richardson (2004) notes the potential of carbon limitation at higher elevation because of a shorter growing season and reduced rates of photosynthesis.

Along with changes in factors that may influence growth, there are documented changes in growth rates with elevation. Whittaker et al. (1974) noted changes in net AGB production with changes in elevation at HBEF. Wood dry weight growth was calculated using the 1961-1965 five year volume increments. This study noted an average of 11.186

Mg $ha^{-1}yr^{-1}$ at low elevation sites (550-630 m) and 7.69 Mg $ha^{-1}yr^{-1}$ at high elevation sites (710-785 m). Joshi et al. (2003) documented a decrease in net AGB production at Whiteface Mountain, New York from 4 Mg $ha^{-1}yr^{-1}$ at 600 m to 3.3 Mg $ha^{-1}yr^{-1}$ at 1000 m. The differences between these two estimates may be related to the different methods used to calculate values. In addition to documented changes in growth with elevation are noted growth-related factors that also vary with elevation. Temperature gradients in the White Mountains have a documented decline of 6.4° per kilometer (km) altitude (0.0064° per meter) (Reiners et al. 1984). Growing degree days have also been established to have a linear relationship with altitude, decreasing at a rate of approximately 1.3 days per meter (Reiners et al. 1984). In a study of northern and southern hemisphere extratropical forests, seventy-nine percent of the global variability of forest line elevation has been attributed to thermal variability (Jobbagy and Jackson 2000).

Another major set of hypotheses for decreased AGB at elevation is related to mortality and the factors that influence it. Elevation is a large factor in determining which trees are affected by large disturbance events such as the ice storm that hit the northeast U.S. in January of 1997. In this event, Rhoads et al. (2002) documented that damage increased with elevation, with damage only occurring above 600 m. Using a Rhoads et al. (2002) equation describing the relationship between elevation and ice thickness, ice is only present on branches above 600 m at 6 millimeters (mm) thickness, increasing to 14 mm, 13 mm, and 6 mm at 700, 800, and 900 m elevation respectively. This study notes that weighted damage class increased with increasing ice thickness. In studies of effects of the 1938 hurricane on Hubbard Brook, 49 years after the disturbance average basal area

was still lower and stem density was higher in the hurricane damaged sites (Merrens and Peart 1992). In Borneo, Gale and Hall (2001) found that in general, the proportion of standing deaths increased with a gain in elevation while uprooting proportions demonstrated a decline with increases in elevation. Slope had little effect on the proportions of snapped trees. In the Rocky Mountains, wind damage to high elevation conifer needles has been documented to wear away the cuticle through windborne ice crystal abrasion. Winter dehydration and death may be a direct result of this type of damage (Hadley and Smith 1986).

HBEF is an intensely studied site well suited to examining these patterns and their causes. Numerous trends have been documented, such as the decrease in average tree height and AGB with increases in elevation (Bohrmann et al. 1970, Whittaker et al. 1974). Allometric equations for tree species have been established (Whittaker et al. 1974, Siccama et al. 1994) to enable future researchers to estimate factors such as AGB through measurements such as height and diameter at breast height (DBH) which are simpler to collect. Schwartz et al. (2003) describes factors controlling spatial variation of tree species abundance at Hubbard Brook. Schwarz et al. (2003) notes that elevation is the most important topoedaphic factor controlling species abundance patterns (Figure 1a). Elevation has been noted to be the primary gradient of spatial variation in biomass at HBEF with an average AGB decline of 35% with an increase of 700 m elevation (Fahey et al. 2005).

Changes in AGB with elevation can be explained at many different levels and by many different factors. In order to better understand the observed trend of decreased AGB with elevation at Hubbard Brook, we have partitioned these hypotheses into four general categories (Figure 2). The first, 'Ecosystem Structure' includes factors such as species composition, DBH, stem density, and changes in allometry. For example, changes in ecosystem structure with elevation may include trees becoming smaller or forests having lower stem densities at higher elevations. The second category, 'Growth and Mortality', includes changes in the relative rates of tree growth and mortality along an elevation gradient. Under this category, tree growth rates may decline, and/or tree mortality may increase with elevation due to disturbance or land use. The third category 'Direct Environmental Factors' addresses environmental factors that have a direct impact on forest stand growth and mortality. These 'Direct' factors include temperature, precipitation, humidity, wind, growing season length, and nutrient availability. Increases in wind speed, and decreases in temperature and growing season length at higher elevations may explain the trend of decreased AGB and height with elevation. The final category 'Indirect Environmental Factors' are those that have an indirect impact on changes in forest dynamics with elevation such as slope, aspect, soil type and soil depth. Increases in slope and decreases in soil depth may impact changes in AGB and height with elevation at Hubbard Brook. Hypotheses in different categories can be causally related and thus simultaneously true.

Our approach was to complete analyses of both field and remote sensing data. These data included individual tree and plot level data, and LiDar and AVIRIS remote sensing data,

and the collection of additional tree cores. Most of our regressions were versus elevation because elevation is such a significant predictor of AGB and height. Hubbard Brook, like most forested landscapes has a lot of heterogeneity, with a number of factors that contribute to this heterogeneity. Fortunately, there are a lot of data points available. These factors combine in a way so that we have a lot of analyses with significant relationships that explain a relatively small amount of variation.

Site Description

The focal study site is Hubbard Brook Experimental Forest (HBEF) a northern hardwood forest located within the White Mountain National Forest in central New Hampshire, near West Thornton (geographic center of HBEF is 43°56'N, 71°45'W). HBEF is a 3,037 hectare valley and ranges from 222 to 1015 m elevation (Schwarz et al. 2003, Fahey et al. 2005). This site was chosen because of its large amount of existing data and because of its proximity to University of New Hampshire. HBEF is a historical Long Term Ecological Research (LTER) site and has been the focus of extensive studies in the 50 years since its establishment in 1955 by the United States Department of Agriculture Forest Service. Research is focused on forest and watershed dynamics on a long term time scale and there are many existing relevant LiDar data, hyperspectral data, field data, and model simulations. Much research has been done on a watershed scale through the comparison of manipulated (clear-cut or selectively logged) and undisturbed watersheds (Likens et al. 1994, 1998). There is a gridded system of plots that are distributed evenly and are arranged along north-south transects throughout the entire valley (Figure 3). The

431 Valley plots, also known as the "Schwarz" plots, are each 500 m^2 and range in elevation from 245 to 910 m above sea level. They were established as tagged tree plots in 1995 through 1998 and are being re-measured during the summers of 2005 and 2006.

The Valley plots were established as tagged tree plots from 1995 to 1998 and associated data was collected on plot level information, canopy tree measurements, sapling and seedling measurements, and soil measurements. Plot level information includes transect number, plot number, elevation, aspect, and slope. Canopy tree measurements were made on all trees with diameter at breast height (DBH) greater than or equal to 10 centimeters (cm). These trees were measured and tagged, identified to species, assigned a crown value, and cored. Sapling and seedling measurements included an analysis of understory regeneration in a 1 by 24 m plot within each Valley plot where all live saplings were identified, counted, and tallied according to size class (Schwarz et al. 2003).

CHAPTER II

ANALYSIS OF FACTORS EXPLAINING AGB AND HEIGHT DECLINE WITH ELEVATION

The primary pattern this study is attempting to explain is the decline of average AGB and height with elevation at Hubbard Brook. Plot level data demonstrate a 44% decrease in AGB (Figure 1a), a 39% decrease in LiDar measured tree height (Figure 1b), and a 42% decrease in field measured tree height (Figure 1c) with an increase of 600 m in elevation. To address the observed pattern of decreased height and biomass at higher elevation at Hubbard Brook data were collected and analyzed. The following four categories of hypotheses: 'Ecosystem Structure', 'Growth and Mortality', 'Direct Environmental Factors', and 'Indirect Environmental Factors' (Figure 2) address these trends on several different levels in an attempt to better understand this specific aspect of fine scale heterogeneity at Hubbard Brook.

Ecosystem Structure

One category of explanation for the trend of decreased AGB and decreased height with elevation at HBEF includes the changes that occur to ecosystem structure. The pattern of AGB with elevation is a direct result of changes in DBH, stem density, and species composition because the plot AGB values are calculated as a function of individual tree DBH and species specific allometries. Because the AGB for each individual tree within a plot is added to get the plot total AGB, the density of trees on each plot is also important. Three main questions relate to changes in ecosystem structure with elevation at Hubbard Brook: Are trees smaller with increases in elevation at Hubbard Brook? Are the stem densities of the plots decreasing with elevation at Hubbard Brook? Is there an effect of change in allometries with elevation?

To address the first question, we regressed average plot DBH versus elevation. This trend (Figure 4) showed an average decrease of 23 % from 300 to 900 m in elevation. We can infer from this trend that trees are significantly smaller at higher elevations and this may be a possible explanation for the pattern of AGB and height decline with elevation.

To address the second question about changes in stem densities with elevation, we plotted the total number of individuals per plot versus elevation (Figure 5). This plot shows an average increase of 87% in the number of trees (greater than 10 cm DBH) at each 500 m^2

plot between 300 and 900 m elevation. This figure establishes that the decrease in biomass at elevation is not caused by a decrease in the number of trees at elevation. These patterns have been documented previously in the White Mountains at Crawford Notch, where the density of live stems ($\geq$5 cm DBH) generally increased with elevation (Foster and Reiners 1983).

The third question required an analysis of the relationship between allometry and elevation. Changes in allometry may account for the decrease in average tree height with increases in elevation. Cordell et al. (1999) and Meinzer et al. (1984) noted that high elevation plants often exhibit distinct morphology such as dwarfness, compact habit, and small densely pubescent leaves. Tree morphologies are noted to demonstrate shorter, thicker forms with increases in elevation. The length of new twigs produced each year decreases with increases in elevation in certain conifer species in the Rockies (Hansen-Bristow 1986, Schoettle 1990). Elevation specific tree allometries have been developed for HBEF tree species but these allometries are affected by species changes with elevation and may not reflect within species changes in allometry with elevation (Whittaker et al. 1974). Within species change in allometry has been documented within Watershed 6 of HBEF where the average height of a 50 cm DBH American beech declines almost 30% with an increase of 300 m elevation. Sugar maple and yellow birch demonstrate an approximate 20% decline with a 300 m increase in elevation (Fahey et al. 2005).

Changes in allometry may explain the trend of decreased AGB with elevation. The AGB trend with elevation, the field height trend with elevation, the LiDar height trend with elevation all show very similar declines (44%, 39%, and 42% respectively between 300 and 900 m). These data may indicate that in general, changes in elevation are not accompanied by significant changes in allometry. However, change in elevation is accompanied by a change in species composition (Figure 6), and changing allometries that are associated with changes in species composition may impact the trend of declining AGB with elevation. To evaluate the magnitude of this effect on the trend in AGB, a single allometry (Yellow Birch) was applied to all tree DBH measurements to see if this affected the trend of biomass decline with elevation. We repeated plot level AGB estimates using this single allometry for all stems. The resulting plot (Figure 7) demonstrates a trend of 35% decline average AGB from 300 to 900 m, compared the actual total decline which is 44% (Figure 1a). This indicates that species specific allometry does have an impact on changes in AGB with elevation as 9% out of 44% is approximately 20% of the total trend in AGB decline. The remaining 80% of AGB change with elevation can be attributed to changes in DBH and stem density.

Statistical significance of these trends was evaluated using standard regression technique JMP 6 statistical software t-test. It appears that the most significant factor responsible for the decline of AGB with elevation is the decrease in plot average DBH with increases in elevation. This raises the next category of hypotheses to address the question of why trees are smaller at elevation.

Growth and Mortality

A second category for explanation for changes in AGB and height with elevation is related to growth and mortality rates. Simple models show that a decrease in biomass may either be a function of decreased growth or increased mortality. Decreased growth rates at higher elevation plots may be responsible for the trend of smaller trees at higher elevations. Alternatively, an increased rate of mortality, as caused by both natural (ie. hurricanes, ice storms) or human (ie. logging, management) disturbances could account for the decline in average tree size with elevation. These phenomena may also act together to explain the change in tree size with elevation. The primary method for establishing patterns of growth and mortality was the measurement and analysis of tree cores. There are two types of tree core data for HBEF, short cores for analysis of growth, and long cores for analysis of growth and age. Existing valley wide short cores were collected by Schwarz and crew on each of the trees larger than ten cm DBH within the 381 plots. This is a total of 10,764 short cores. Existing valley wide tree age data from HBEF consists of approximately one to two long cores collected from each Schwarz plot (total of 371 cores).

Because of numerous studies that document decreased rates of growth with elevation (Whittaker et al. 1974, Korner 1999, Oleksyn et al. 2002, Joshi et al. 2003, Fahey et al. 2005), it was important to investigate the effect of changes in rates of growth on the decline in average AGB with elevation. Two separate approaches were used to isolate

plot level growth. The first entailed calculating average net growth by dividing the AGB of each plot by the corresponding estimated age of each plot (Equation 1).

$$\overline{NetGrowth} = \frac{\overline{AGB}}{\overline{Age}} \qquad (1)$$

The plot total AGB was calculated by adding up the AGB of each individual tree larger than 10 cm DBH using species specific allometries (Siccama et al. 1994, Whittaker et al. 1974) (data courtesy Paul Schwarz). Plot age was established based on the age of the long core(s) for each plot, and is in effect an estimate of minimum age. A similar method for estimating an annual biomass increment was utilized by Raich et al. 1997 who divided the total aboveground biomass by the age of the underlying lava to estimate net growth. Figure 8a demonstrates the relationship between average net growth and elevation. Based on this figure the average net growth rate decreases by 26% (0.54 Mg $ha^{-1}yr^{-1}$) between 300 and 900 m in elevation.

A second approach estimated growth using a radial increment (RI) method to calculate an annual DBH and AGB for each tree (Equation 2).

$$\overline{RIGrowth} = \frac{\Sigma(\Delta AGBi)}{Nyears}, \quad i = 1 \ldots N\,years,\ N = 5 \qquad (2)$$

A species specific allometry (Siccama et al. 1994, Whittaker et al. 1974) was applied to each tree's annual DBH, providing an annual estimate of AGB for each tree (greater than

10 cm DBH) on each plot. Annual AGB's were differenced to establish a growth metric for each tree. These were summed within plots to determine plot level growth. This number was then divided by plot area to so that the AGB term was in Mg/ha. A similar method utilizing tree core radial increments as a valid means for estimating AGB increments is described by Clark et al. 2001 and is utilized by Joshi et al. 2003. The plot level trend of RI growth versus elevation demonstrates a significant trend of decreasing productivity with increases in elevation (Figure 8b). This figure shows an average decrease of 0.96 Mg $ha^{-1}yr^{-1}$ between 300 and 900 m elevation. This is an average decline of 36 % from 300 to 900 m elevation. The relationship between the two estimates has a slope approximately equal to one (Figure 8c).

Increased rates of mortality at higher elevation sites may be another cause for the trend of decreased AGB and height with elevation. To investigate the effect of plot age-resetting mortality rates on the change in AGB with elevation, it was necessary to establish the differences in plot age. The minimum age for each plot was estimated from the minimum age of the largest red spruce or American beech 1996 (including some 1997) cores collected by Paul Schwarz. The trend in Figure 9a demonstrates a statistically significant decline of an average 25.44 years between 300 and 900 m elevation. Average age declines 18% from 140 years to 114 years. Because these trees were pre-selected to be the single largest surviving tree at each plot, there is a lack of information of the age distribution within the plots. For this reason, we collected additional tree cores from a selection of plots at each elevational band. To establish that this trend was representative

of the plot age, a sub-sample of plots were visited during the summer of 2005 to re-core the six largest trees per plot.

Sampling Design

Our field work began with the identification of 18 Schwarz plots at low, mid, and high elevation (350-450, 550-650, 750-850 m) locations. The collection of approximately 100 long cores was established as a feasible number for the time constraints of this project. Analysis demonstrated the importance of collecting several cores at each plot to eliminate the possibility of "cherry-picking" only the older trees. The collection of three birch cores per plot enabled comparison of growth trends within a single species. Three additional cores were collected from the 3 largest (as determined by DBH) remaining trees on each plot to ensure analyses of canopy trees that are responsible for the LiDar height trend. The plots were evenly distributed across the three elevation bands with six plots at each. By using three separate elevation bands, data was partitioned across elevation. Six mid elevation and five high elevation plots were selected based on availability of existing nitrogen data. The remaining one high elevation plot and six low elevation plots were randomly selected plots whose elevation/height relationship lies within one sigma of the line describing the LiDar height/elevation relationship. Plots were selected to be within one sigma to ensure that the plots sampled are part of the trend that we are evaluating within this study: the pattern of height and biomass decline with increases in elevation at HBEF. A program was used to identify six random height/elevation pairs that fell within one sigma of the line at each elevation band. Once

these random pairs were generated, they were correlated to the LiDar height elevation data to locate the coordinates that best matched each height/elevation pair. Once the coordinates were identified, they were matched to the closest Schwarz plot.

Collection and Analysis of Tree Cores

A total of 108 cores were collected from 18 pre-selected Schwarz plots. At each Schwarz plot, cores, DBH and height measurements were collected from 3 canopy *Betula alleghaniensis* (yellow birch). Yellow birch is the most prevalent tree species by biomass at Hubbard Brook and it is found across all elevational ranges (Schwarz et al. 2003). If there were not three canopy yellow birch within the plot, *Betula papyrifera* (paper birch) was sampled instead, so as to have half the samples from the same genus. If there were not three canopy yellow or paper birch within the plot, plot diameter was extended no more than 20 m to include three yellow birch and/or paper birch. In addition to the three canopy yellow or paper birch, cores, DBH, and height measurements were collected from the remaining three largest canopy trees within the plot (based on DBH measurement). It is important that canopy trees were selected to ensure trees measured were contributing to the LiDar trend. The 108 trees were cored using an increment tree corer. Height and DBH were measured using a laser range finder and DBH tape.

Tree cores were mounted and sanded before being analyzed through use of a dendrochronometer. With the aid of a computer program attached to the microscope,

ring width was measured. The program records the exact distance that cores are moved to match each ring boundary to a specific point on the microscope stage. This records the exact width of each ring to the nearest 0.01 mm. The 108 cores collected were mounted, dried, and analyzed to determine age and radial increment growth rate.

These tree cores were analyzed to determine if the age trend established by Schwarz's cores is representative of plot level age. The minimum age of the six largest trees on each re-sampled plot exhibits a relationship with elevation (Figure 9b) that is very similar to the previously established relationship (Figure 9a) between plot age and elevation (slopes equal to -0.0434 and -0.0424 respectively). Average age declines 19% from 139 years to 113 years (Figure 9b) which is in very close agreement with previous data which demonstrates an average age decline of 18% from 140 years to 114 years (Figure 9a).

Because there is evidence for changes in both net growth and plot age-resetting mortality operating, it was necessary to partition the relative importance of each. We developed a statistical model to quantify the relative importance of net growth and age-resetting mortality in the AGB trend with elevation.

$$\Delta AGB_{Total} = NetGrowth_{300} \times Age_{300} - NetGrowth_{900} \times Age_{900} \qquad (3a)$$

The ΔAGB_{Total} term represents the average change in AGB from 300 m to 900 m, 114.96 Mg/ha. The values for the average age and elevation specific age were derived from the plot of the minimum age of each long core versus elevation. Equation (3a) represents the

total change in AGB with elevation, and the contribution of both changes in rates of net growth and mortality. Thus, both the net growth and the age terms are elevation specific. To partition the effect of changes in net growth and mortality, an additional two equations were derived.

$$\Delta AGB_{Mortality} = \overline{NetGrowth} \times Age_{300} - \overline{NetGrowth} \times Age_{900} \qquad (3b)$$

$$\Delta AGB_{Growth} = NetGrowth_{300} \times \overline{Age} - NetGrowth_{900} \times \overline{Age} \qquad (3c)$$

Equation (3b) represents the portion of the total change in AGB with elevation which can be attributed to changes in age-resetting mortality with elevation. In this equation, the age term is elevation dependent. Net growth term in this equation is equal to the average net growth across the elevational range.

Equation (3c) isolates the effects of changes in net growth. Only the net growth term is elevation specific while the age term is the average age across all elevations. The third equation represents the portion of the total change in AGB with elevation which can be attributed to changes in rates of net growth.

Applying this model to the data from HBEF results in a partitioning of the decline to 60% net growth and 40% age (Figure 10). Having established the relative magnitude of these effects, the next question asked was: What factors are causing these growth and age effects?

Direct and Indirect Environmental Effects

Direct Environmental Effects

Many environmental factors that change with elevation may have a direct effect on tree growth rates and mortality. Some examples of direct environmental factors that may be related to changes in elevation are: temperature, precipitation, humidity, wind, growing season length, and nutrient availability (ie. nitrogen) (Barrick and Schoettle 1996, Joshi et al. 2003, Kitayama et al. 2002, Richardson et al. 2004). In the White Mountains, temperature declines 0.64° per meter altitude (Reiners et al. 1984). Growing degree days in the White Mountains have a linear relationship with altitude, decreasing approximately 1.3 days per meter (Reiners et al. 1984).

To investigate the impacts of climate on rates of growth, we analyzed meteorological data available through the 22 rain gauges at Hubbard Brook. Using these data, we evaluated changes in temperature and precipitation with elevation (Figure 11). Meteorological station data indicates a positive relationship between average annual precipitation and elevation, with an increase in approximately 22 mm between 300 and 900 m elevation (15% of the overall average precipitation of 145 mm). This suggests that water limitation may not explain decreased rates of growth at higher elevation sites. However, the depth and composition of the soils may impact the water availability at the higher elevation sites (Salter 1940, Sollins 1998). Temperature has an inverse relationship with elevation,

with a decrease in approximately 3° Celsius average minimum temperature from 300 to 900 m. The average annual temperature decreases approximately 3.5° Celsius between 300 and 900 m. In general, rates of photosynthesis increase with increases in temperature until a peak at approximately 30° Celsius and subsequent decline with any further increases in temperature (Taiz and Zeiger 2002). It is thus possible that temperature variation may explain some of the variation in net growth.

Hyperspectral indices for factors that limit or indicate limited growth were assessed for relevance to LiDar height data at Hubbard Brook. Previous work with Airborne Visible/Infrared Imaging Spectrometer (AVIRIS) hyperspectral remote sensing data has demonstrated capabilities to estimate aboveground forest productivity (Smith et al. 2002, Smith et al. 2003, Turner et al. 2004.) To address the hypothesis of changes in foliar nutrients with elevation and to evaluate the potential use of hyperspectral remote sensing data for interpreting changes in height and AGB at HBEF, an unprocessed 2003 AVIRIS scene was acquired. This AVIRIS scene was processed using an atmospheric correction program, Atmospheric CORrection Now (ACORN). A 190 band subset of the original 224 band image was created including separate wavelength, gain, and offset files. The image was also subset in ENvironment for Visualizing Images (ENVI) software to eliminate data that that was not within or close to the Hubbard Brook boundary. ACORN mode 1.5 was run on the 2003 AVIRIS scene. Once the scene was atmospherically corrected, Leica Geosystems Geospatial Imaging: ERDAS IMAGINE was used for geometric correction. Arc GIS was used to specify the Valley plots and the 2006 re-sampled plots within Hubbard Brook (Figure 12a). A linear relationship was developed

between field measured foliar N and spectral response (AVIRIS) based on methods described in Smith et al. 2002. This linear equation was applied to entire image to predict foliar N for each pixel across entire image. A nitrogen estimate previously calculated by Smith et al. (2002) utilizes partial least squares regression to relate AVIRIS spectral response to whole-canopy N concentration. This was applied to the processed HBEF AVIRIS image and the AVIRIS derived N concentration value was extracted for each Schwarz plot. These N values show a statistically significant declining trend with elevation from 2.20 to 1.78 (% dry weight foliar N concentration). This is an approximate decline of 19% foliar N from 300 to 900 m (Figure 12b). This trend has a similar slope to the relationship between field tested N values and elevation (Figure 12c). (Refer to Appendix III). Since N concentration typically decreases with elevation (Ollinger and Smith 2005), this trend at Hubbard Brook can be explained by the change in species composition as conifers have lower foliar N concentrations than hardwoods.

Evaluating changes in growing season length has provided a metric for analyzing the combined effects of changes in climate (precipitation, temperature, humidity, and wind) with elevation on the average plot AGB. Changes in growing season length may provide information on the impacts of these variables on canopy growth dynamics (Zhang et al. 2004, Zhang et al. 2005). To assess changes in growing season length, phenology data have been collected at nine separate locations at HBEF since 1989. These sites monitored categories of phenology from 0 (winter condition, all leaves off) to 4 (summer condition, all leaves on). Figure 13 demonstrates the different growing season lengths at these sites which include American beech, sugar maple, and yellow birch. For 1999,

there was an average difference of 20.3 days of growing season length between 253 and 802 m elevation sites. Based on the relationship between growing season length and elevation, there are an average of 26.1 days difference between 300 and 900 m elevation and an approximate 16% decline over the elevation range.

An additional analysis of growing season length utilized the TIMESAT software for analyzing 2002 MODIS data (Jonsson and Eklundh 2004, Jonsson and Eklundh 2006) from NASA's Terra satellite. This analysis was performed by Jeff Morisette and his team from NASA's GSFC. This team provided a 500 m resolution image of HBEF with spatial reference information attached to growing season values. This image was overlaid with a DEM elevation image in Arc GIS to correlate each pixel's growing season length (days) with elevation (m). The 2002 MODIS derived growing season length versus elevation demonstrates a decline from 217 days at 300 m to 181 days at 900 m. MODIS derived growing season length shows the same 16% decline between 300 and 900 m elevation as the field observation growing season estimate. The MODIS estimate may have an overall longer growing season length because it encompassed the entire HBEF watershed which includes all species types, while the field estimates only monitored deciduous sites.

Many environmental factors may influence rates of mortality to decrease AGB and height at high elevations. Increased rates of mortality at higher elevations could be a result of poorer growing conditions or increased rates of disturbance. Pederson (1998) found that for oaks in seven Midwestern forests, tree mortality was usually a long process that

involves a combination of environmental stresses. Studies have documented increased rates of disturbance at higher elevation sites (Gale and Hall 2001). In assessing effects of the 1997 ice storm at HBEF, Rhoads et al. (2002) noted an increase of damage to trees as elevation increased.

Wind speeds during the growing season in the Northeast have documented increases with elevation (Richardson et al. 2004, Sabo 1980). Sabo (1980) suggests that in the White Mountains, mean above-canopy wind speeds increase from 2.7 m/s at 500 m, to 8.3 m/s at 1000m and 12.5 m/s at 1500 m (Richardson et al. 2004). These values are higher than those estimated by Richardson et al. (2004). Based on the Sabo 1980 estimate, the wind speed would increase roughly 7-fold between 300 and 900 m at Hubbard Brook from 0.9733 m per second to 6.8533 m per second. Although the linear relationship between wind speed and elevation is a simplified representation, based on this analysis, it seems likely that changes in wind speed with elevation may have an impact on changes in AGB with elevation through increased rates of disturbance.

In addition to natural disturbances, age related patterns may also be caused by land use history. Records indicate that red spruce trees were selectively logged in the Hubbard Brook valley from 1870 to 1900. Red spruce and hardwoods were extensively logged from 1906 to 1920. A 1919 timber survey of the Hubbard Brook valley indicated that the cutting was especially heavy at the high elevations and in the lower parts of the valley (Peart et al. 1992).

Indirect Environmental Effects

Data on environmental factors that may have indirect relevance to changes in AGB and height with elevation were evaluated in this analysis of our final set of hypotheses. Gridded information on potentially relevant environmental factors, including, aspect, slope, and soil type and depth, was obtained from existing field and remote sensing data. Data on aspect, slope, and elevation has been acquired through the analysis of the 1999 LiDar data set using Arcview. These data have been reaggregated to 0.5 hectare resolution.

Field data on indirect environmental factors at Hubbard Brook were available through Paul Schwarz's data sets. At each plot, Schwarz and crew calculated slope, aspect, average steepness, terrain shape index, and depth to obstruction. This ground data set provides detailed information about topography at each of the 371 valley wide plots. Additional data collected by Paul Schwarz established a mean soil depth for each plot by plunging a steel probe into the ground along an East-West diameter of each plot (Schwarz et al. 2003). These data points show an overall decrease in soil depth as elevation increases (Figure 14a). This may indicate that a decrease in average soil depth is related to the decline in average AGB and height with elevation, perhaps because of decreased soil moisture or decreased stability for larger trees. Soils may be important to the trend of AGB with elevation because changes in soils have been associated with changes in aboveground NPP (Bormann and Sidle 1990). The frequency of different soil types change with elevation at HBEF. Figure 14b was created using GIS data available on the

HBEF data website. These data are digitized from a 1955 reconnaissance soil survey. The soils were classified as either Canaan-Shapleigh, Hermon-Waumbek, Leicester-Whitman, Lyman-Hollis, Berkshire-Peru, or Colton-Duane according to texture, drainage, and relative amounts of rock on the surface. This figure shows a marked change in the frequency of each soil type between the three elevation bands.

Our analysis of LiDar canopy height and slope data indicates no significant relationship between the canopy height and slope. Studies have noted that aspect plays a role in ice storm damage to forests. Bernhardt et al. 2003 described damage from the 1998 ice-storm at HBEF as limited to south-facing watersheds. Aspect does appear to have a significant relationship with height along an elevational gradient (Figure 15a), especially at high elevation sites (Figure 15b). At low elevation sites, the graph of tree height versus aspect does not demonstrate a statistically significant relationship (Figure 15d). At mid and high elevation sites, south facing slopes have lower heights as noted by a U-shaped curve with the south facing (180-210 degrees) points associated with the lowest average heights (Figures 15b and 15c). Statistical significance of these trends was evaluated using standard regression technique JMP 6 statistical software t-test.

CHAPTER III

DISCUSSION

To better understand the observed trend of decreased AGB and height with elevation at Hubbard Brook, we have examined hypotheses within four categories: 'Ecosystem Structure', 'Growth and Mortality', 'Direct Environmental Factors', and 'Indirect Environmental Factors'. These different scales of analyses have enabled us to address several levels of factors related to changes in AGB and height with elevation (Figure 16). We have established that a decrease in the plot average DBH is the primary cause responsible for the decline in AGB and height with elevation. The relative importance of changes in net growth and plot age-resetting mortality are 60% and 40% respectively. AVIRIS-derived N measurements declined by 19% between 300 and 900 m. Average annual temperature declined by 3.5° C and growing season length by 26.1 days (field data) or 35.5 (MODIS data) days between 300 and 900 m elevation. Aspect may have a significant relationship with tree height, while slope does not. Average soil depth demonstrates an average decline of 56% from 47 cm to 27 cm with increases in elevation, and soil types transition between low, mid, and high elevation sites. Explanations from

these four different categories can be simultaneously true. For example, based on our study results, higher elevation stands have smaller, slower growing trees which have higher rates of mortality. These stands are also associated with decreased temperatures, shorter growing seasons, decreased foliar N, and decreased soil depth. Elevation is the best predictor of all of these changes and an ecosystem model can combine all of these factors.

Most of our regressions are by elevation because it is such a significant factor for predicting AGB. In order to understand whether or not these factors actually explain changes in AGB per se, these relationships were directly assessed, and in fact many do (Figure 17). Virtually all of the factors that we analyzed were significant with elevation were significant also with AGB with age as the one exception. This may be because while elevation is a significant predictor of age, it is one of the weaker hypotheses. Why age became non-significant with AGB is worthy of further investigation. Also, the relationships between these different factors such as growth and foliar N (Figure 18) will be investigated further.

Understanding the observed biomass and height variations at elevation has important applications in carbon cycle modeling. A potential application of this information is the height structured ecosystem demography (ED) model, which can use tree height data as an input to project the future growth and carbon storage of that particular tree (Moorcroft et al. 2001, Hurtt et al. 2002, Hurtt et al. 2004). This research is proceeding towards the development of a new version of ED that is parameterized through a review of past work

at HBEF in order to better understand the relative importance of different possible hypotheses for the decrease in average AGB with elevation. This model could utilize available soil, climate, and hyperspectral data to predict future carbon stocks and fluxes. Further studies to disentangle the relative influence of these environmental factors on rates of growth and mortality will be necessary for application to this model. Key environmental factors such as temperature and foliar nitrogen concentration could be included in growth predictions.

NASA's Laser Vegetation Imaging Sensor (LVIS) which produces LiDar remote sensing data can establish a tree height data set for use as a model input. In 1999 and 2003, NASA's Laser LVIS, an airborne laser altimeter system, obtained sub-canopy and canopy-top topography data for HBEF. LiDar remote sensing can provide important information on canopy topography at a large spatial scale. However, it is important when determining the rate of future carbon assimilation of a short tree to consider why the tree height is low. A short tree height may be short because it is young and therefore gaining carbon quickly. It may also be short because it is limited by some factor which is preventing a normal rate of growth. Trees at higher elevation typically demonstrate shorter heights. Because of the very different carbon storage implications of these two separate factors, it is necessary to determine what factors are most influential in tree height variations with elevation. It is important to understand what is responsible for the pattern of decreased biomass and height with increases of elevation at HBEF. This study has assigned quantitative values to the relative importance of growth and mortality and has further analyzed the environmental factors such as foliar N, temperature, growing

season, aspect, slope, and soils that may influence the decrease of plot level AGB and height with elevation.

AVIRIS hyperspectral data may be used to better interpret LiDar data before incorporation in models. Hyperspectral data and software may be incorporated to evaluate factors such as productivity, water content, and stand age within plots exhibiting lower height. By using LiDar to map vegetation structure, and optical remote sensing methods to map vegetation condition (age, health, productivity), better interpretation of LiDar height measurements may be possible (Lefsky et al. 2005). This would lead to more accurate predictions of forest growth and carbon stocks and fluxes. Using LiDar and hyperspectral data it may be possible to apply the pertinent factors that limit height to a much broader spatial scale. There is a broad index of hyperspectral data throughout the White Mountain region and much of New England. At present, hyperspectral data is available at all northeast locations of LiDar data sets, which include HBEF LTER, Bartlett Experimental Forest, NH, Harvard Forest LTER, MA, Penobscot Experimental Forest, ME, and Howland Forest, ME.

Several priorities for future research were identified during the completion of this study. In particular, one challenge is the partitioning of the net growth term into separate mortality and growth terms. Because only a 5 year time scale was used for determination of RI growth rate, we may not have been able to accurately estimate the influence of mortality. If we were able to acquire plot level RI growth data for the entire length of stand age, the RI growth rate should demonstrate a lower rate than the net growth rate

determined by dividing plot AGB/plot age. The difference between the two may indicate the rate of mortality experienced at each plot. In the future, plot level rates of mortality may be more accurately estimated through the re-measurement of the Schwarz plots as will be completed during the summer of 2006 by John Battles and Natalie Solomonoff of UC Berkeley.

Although our growth estimate values are within the expected range described in the literature (Joshi et al. 2003, Brown and Schroeder 1999, Whittaker et al. 1974), they are on the low end of the range. In part this may be because of the inclusion of mortality (both age-resetting and non age-resetting). Also, our values are very similar to the values stated in Joshi et al. (2003) which used the same method based on radial increments that was used for our RI growth estimate. This is perhaps an indication that this method has an underestimation bias. Whittaker's growth estimates are higher than ours (11, 10, and 7.7 Mg $ha^{-1}yr^{-1}$) however of these estimates, only approximately 60% is stem wood, branches, and bark. Thus comparable values to ours are 6.6, 6, and 4.6 Mg $ha^{-1}yr^{-1}$. Whittaker's numbers also include saplings and seedlings which ours do not. Whittaker et al. (1974) states that their estimates of biomass and production were affected by a tendency to overestimate values for stands. All of these explanations for a downward bias in our growth estimates remain consistent across elevations, and in estimating changes between low and high elevations, the relationship should not be affected.

Another challenge for future research is the partitioning of the relative importance of disturbance and land use to the trend of decreased average age with elevation. HBEF

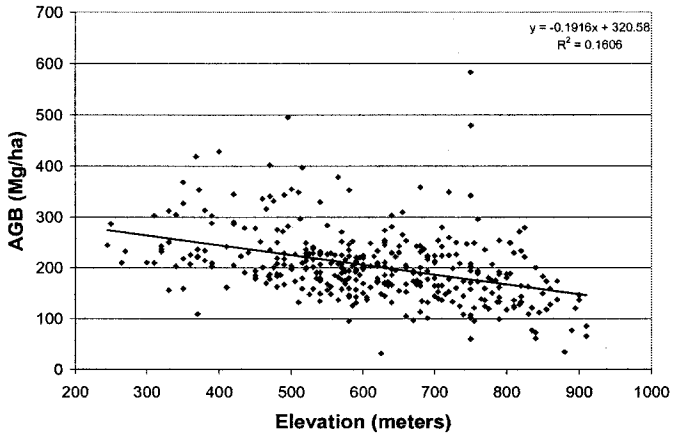
stands are diverse in their disturbance history (Schwarz et al. 2001). Previous studies have established the importance of changes in rates of disturbance with elevation (Rhoads et al. 2002). However, the importance of land use in determining stand age and rates of mortality cannot be overlooked based on information available regarding the logging history at HBEF. Logging history is broadly consistent with and may explain the elevational age trend (Peart et al. 1992). It is important to include the effects of land use history and natural disturbance within a mechanistic model. If it is a disturbance driven trend, an accurate disturbance term must be included in the model because natural disturbance events will occur again in the future. However, land use caused mortality events may not need to be included in predictions of future stocks and fluxes since land use changes will only affect the managed watersheds at HBEF which only represent 10% of the land area. Questions may be addressed through incorporation of existing land use history data and the continued measurement of disturbance events' effects on tree mortality and growth.

Results from this study provide detail to the pattern of AGB and height decline with elevation at Hubbard Brook and improve understanding of carbon stocks and fluxes. This study was designed to provide an improved understanding of patterns of carbon stocks and fluxes on a heterogeneous landscape. The stocks and fluxes of carbon are important to both national funding agencies and international policy and assessments. A better understanding of carbon stocks within the terrestrial environment is of key interest to the Intergovernmental Panel on Climate Change (IPCC Third Assessment Report: Climate Change 2001), the International Geosphere-Biosphere Programme (IGBP

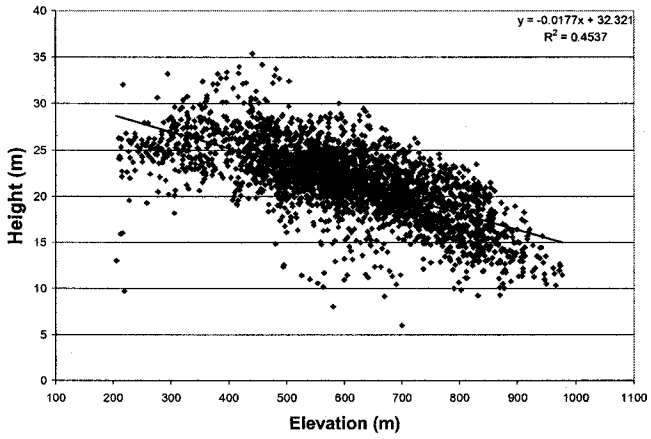
Annual Report 2003 IGBP Secretariat), the North American Carbon Program (NACP), and NASA.

FIGURES

a)



b)



c)

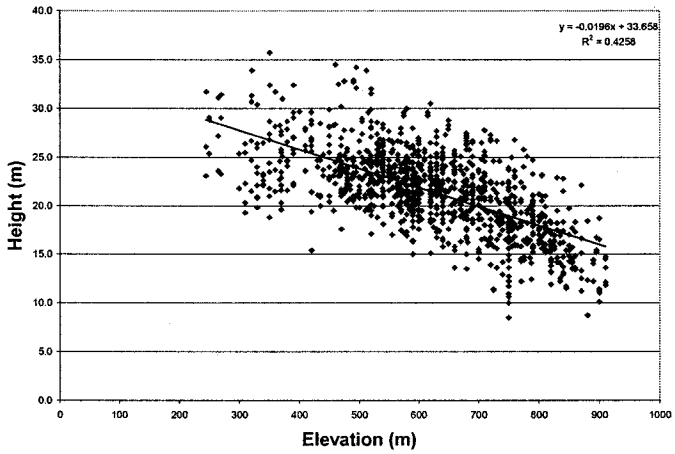


Figure 1a: Plot level AGB versus elevation. Data courtesy Paul Schwarz. T-test p-value<0.0001, N=372. **1b**: LiDar height versus elevation. Data courtesy Ralph Dubayah. T-test p-value<0.0001, N=2959. **1c**: Plot level tree height, Schwarz laser range finder measurements. T-test p-value<0.0001, N=1075.

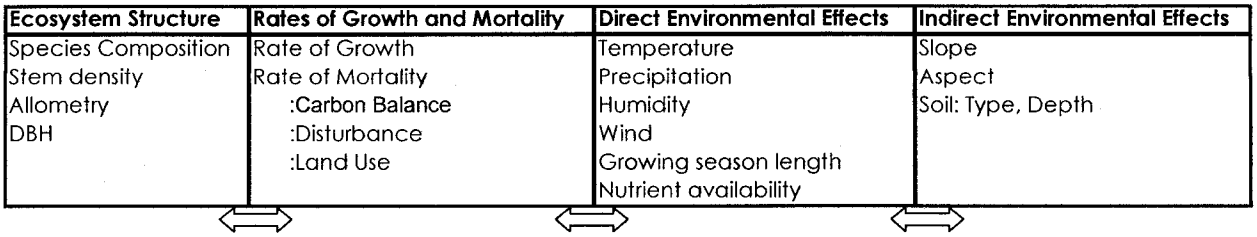


Figure 2: Diagram of levels of understanding changes in AGB and height with elevation at Hubbard Brook. Different tiers for our analysis of fine scale heterogeneity in forest carbon stocks.

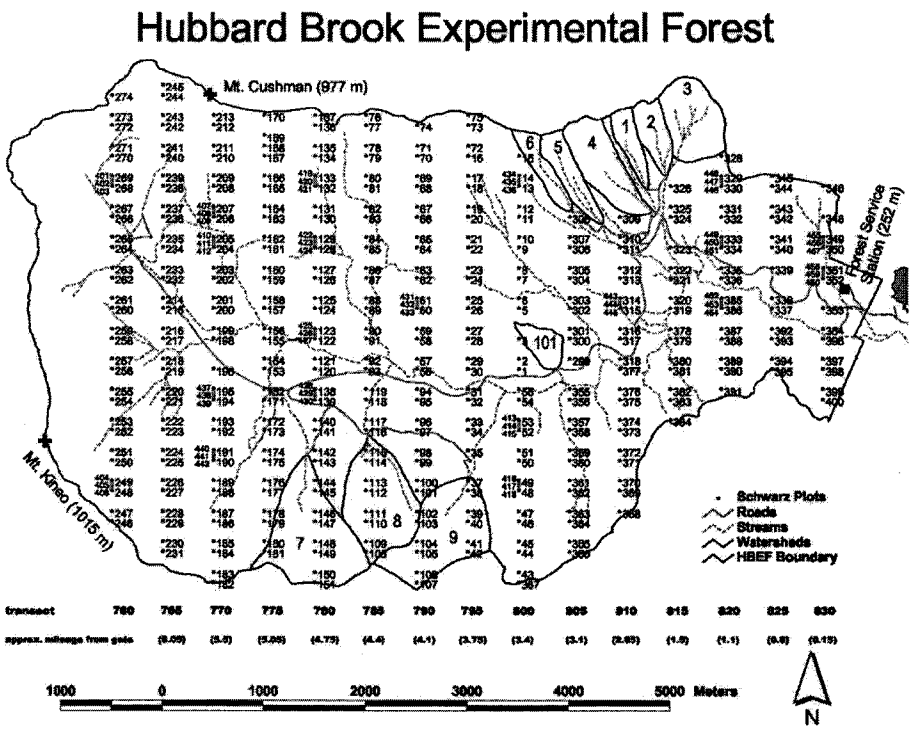


Figure 3: Map of Hubbard Brook and Schwarz Valley Wide plots.

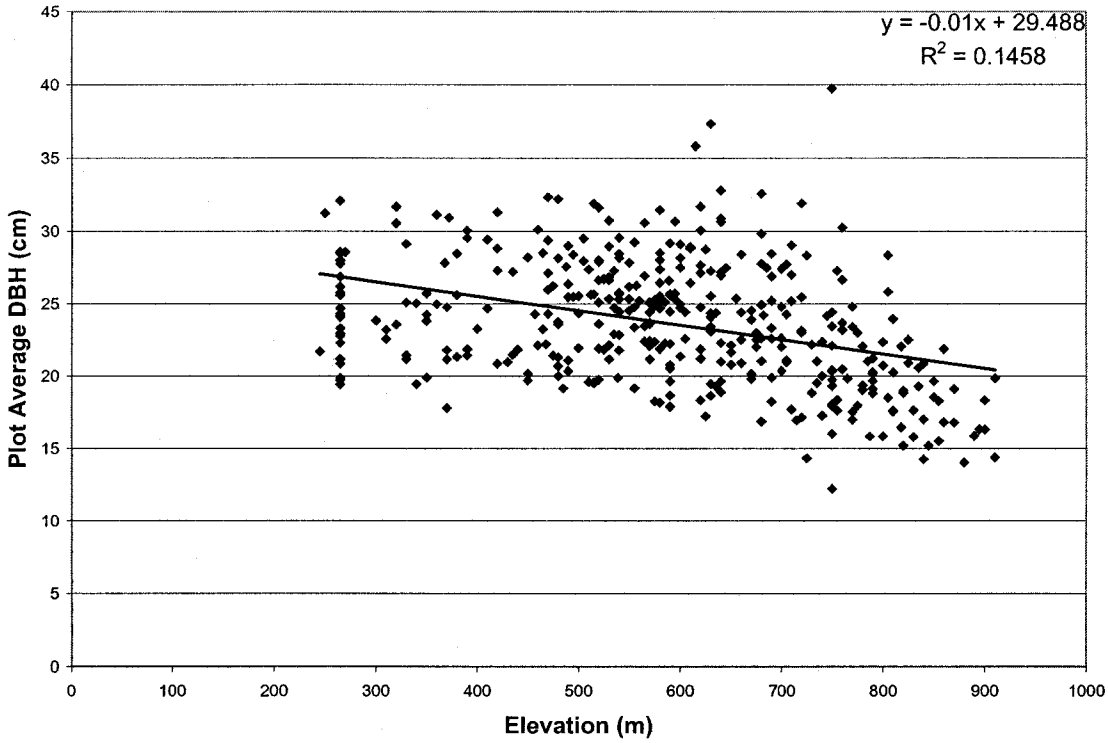


Figure 4: Plot average DBH versus elevation. T-test p-value<0.0001. N = 372.

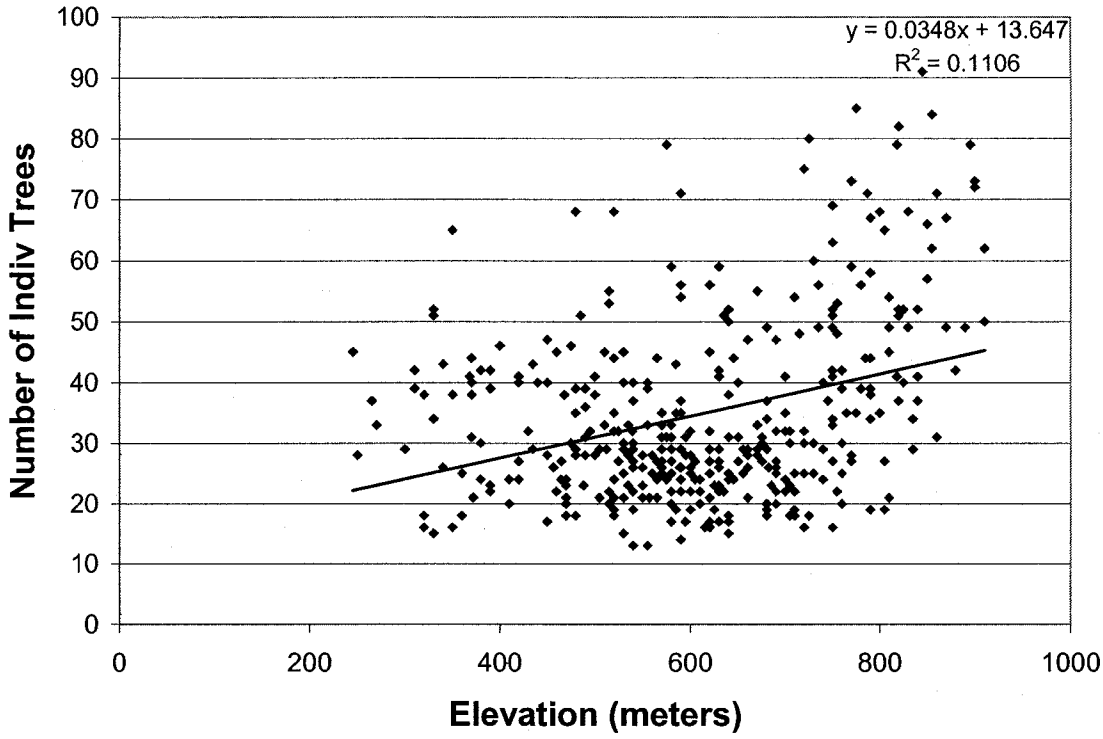


Figure 5: Number of individual trees in each plot versus elevation. T-test p-value<0.0001. N = 372.

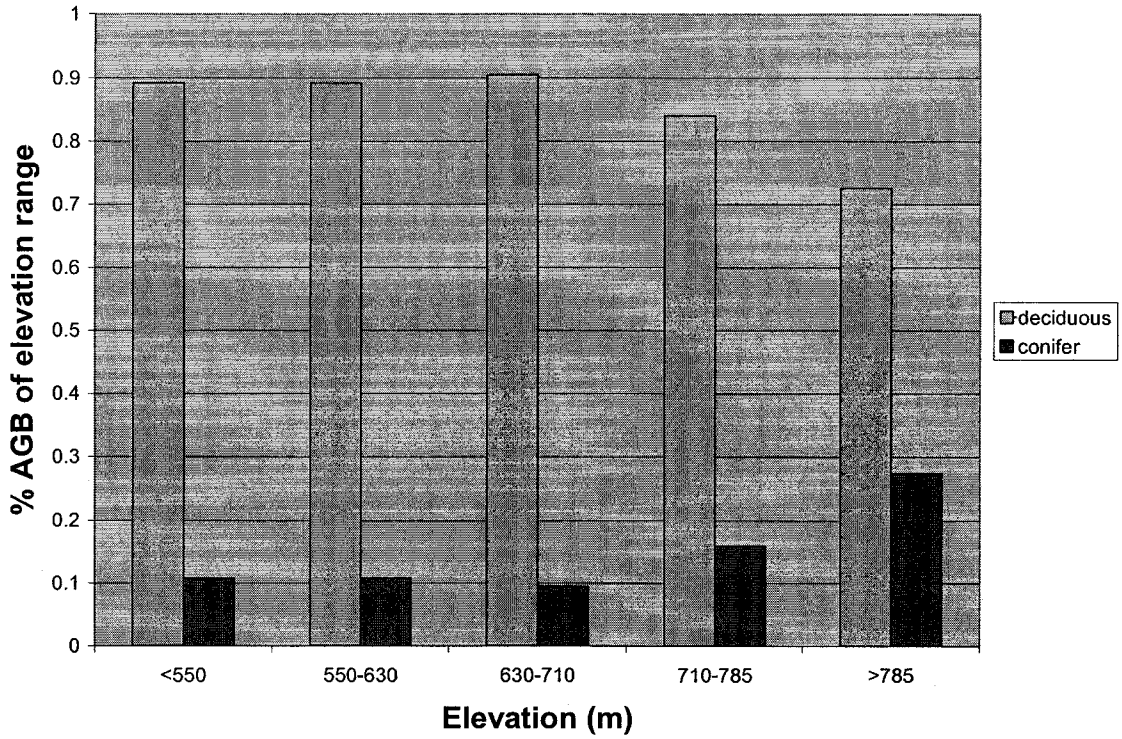


Figure 6: Frequency of coniferous and deciduous species by elevation class. Each elevation band value calculated by dividing AGB of each species type by total AGB at that elevation.

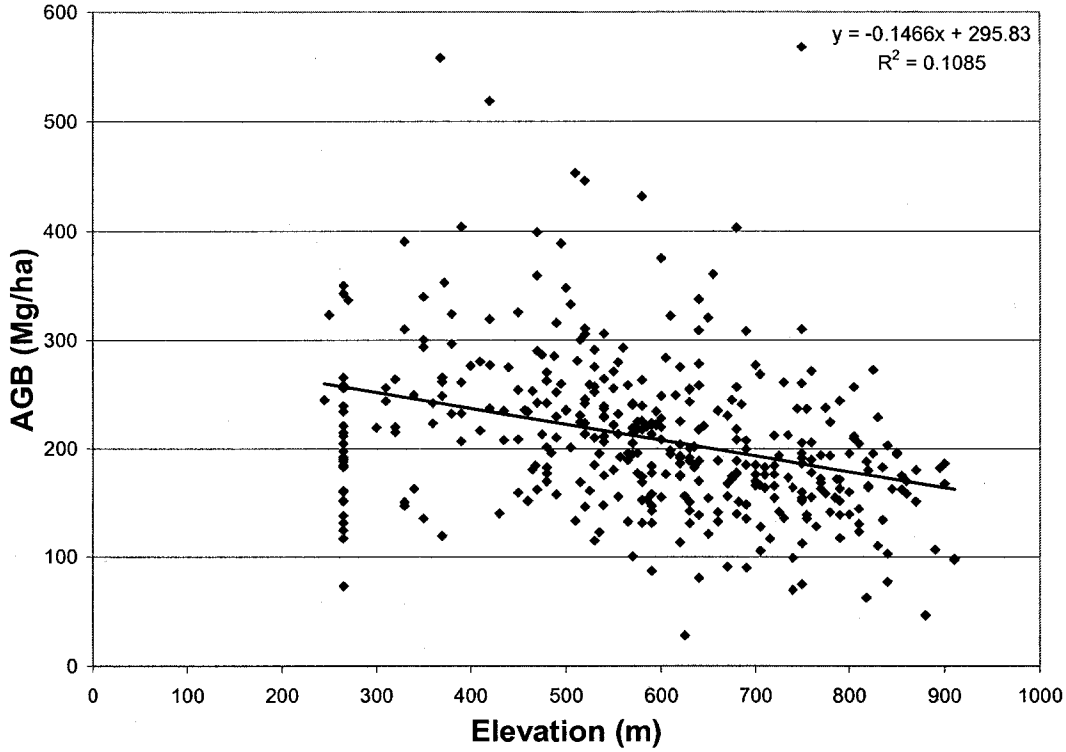
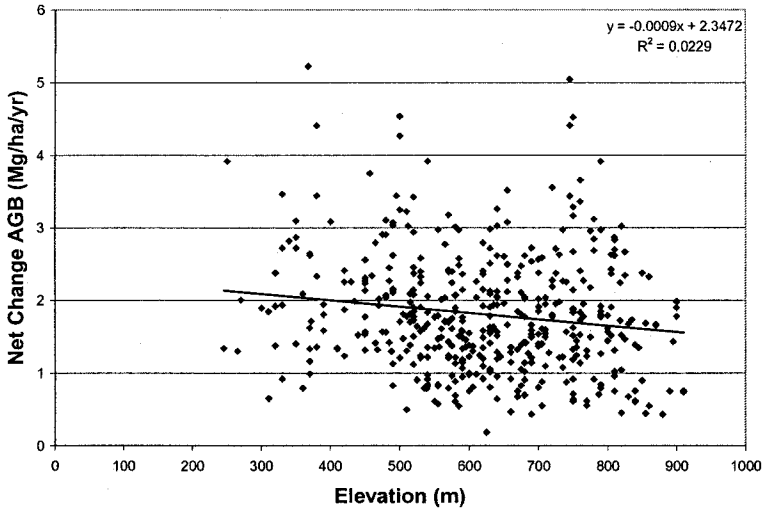
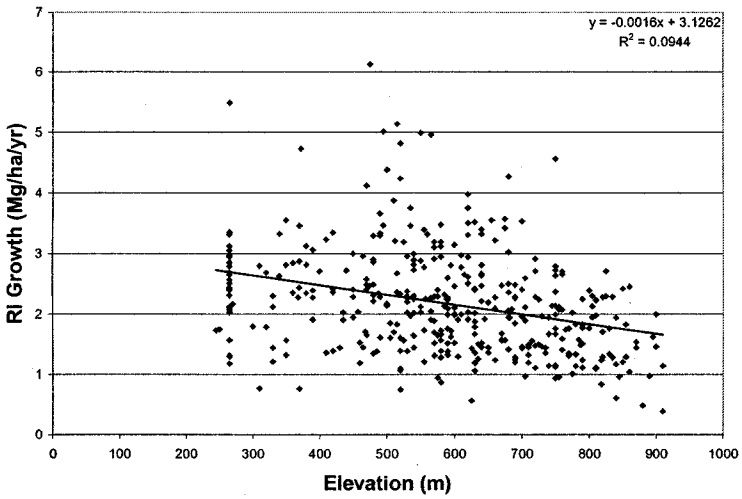


Figure 7: Plot level AGB derived from same application of Yellow Birch allometry to each individual tree's DBH. T-test p-value<0.0001, N=372.

a)



b)



c)

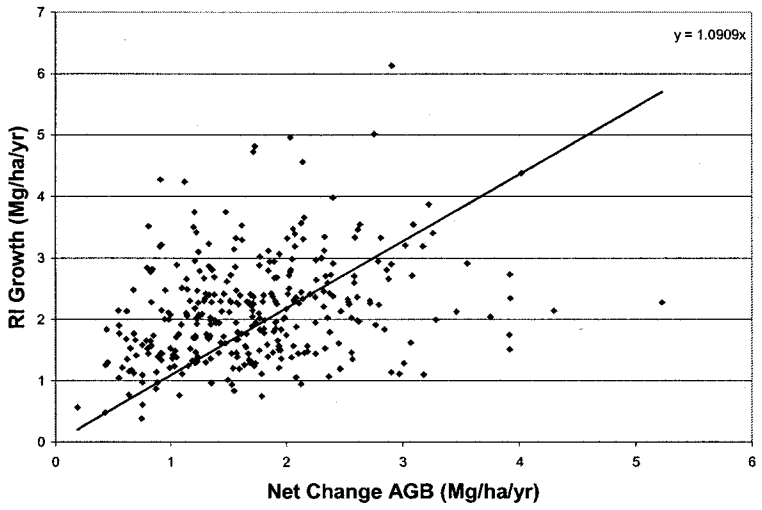
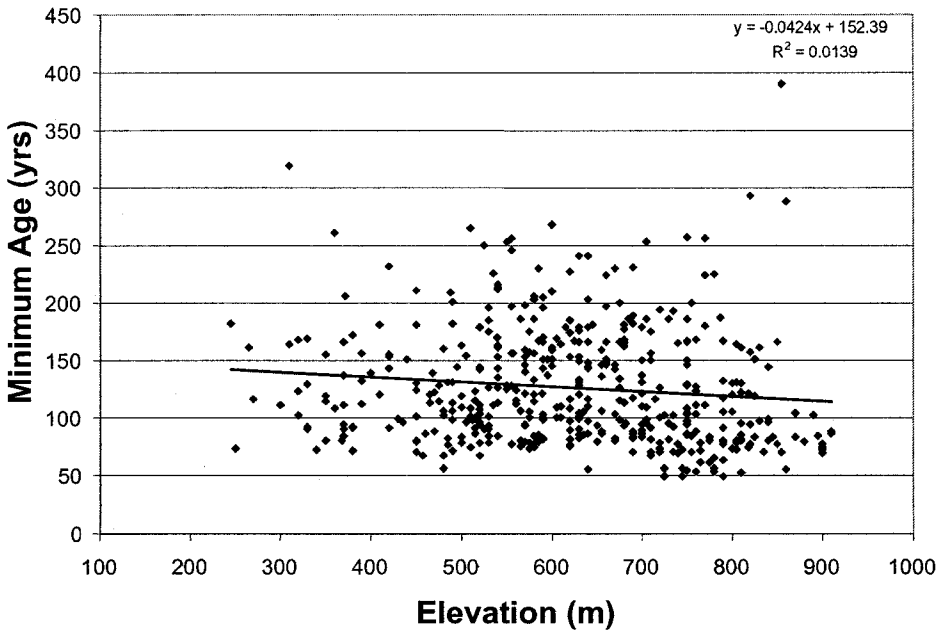


Figure 8a: Rate net AGB accumulation versus elevation. This plot demonstrates the relationship between our growth term and elevation. The rate of net growth decreases by 26% between 300 and 900 meters in elevation. This growth term is derived by dividing the average of AGB per plot by each age. T-test p-value = 0.0013, N=452. **8b**: RI Growth: tree increment core derived plot level 1 year (averaged over 5 years) change in AGB with elevation. This growth measurement shows a decrease of 36% between 300 and 900 meters in elevation.T-test p-value<0.0001, N=382. **8c**: AGB accumulation versus net growth as derived by radial increment. Intercept constrained to 0. T-test p-value<0.0001. N = 329.

a)



b)

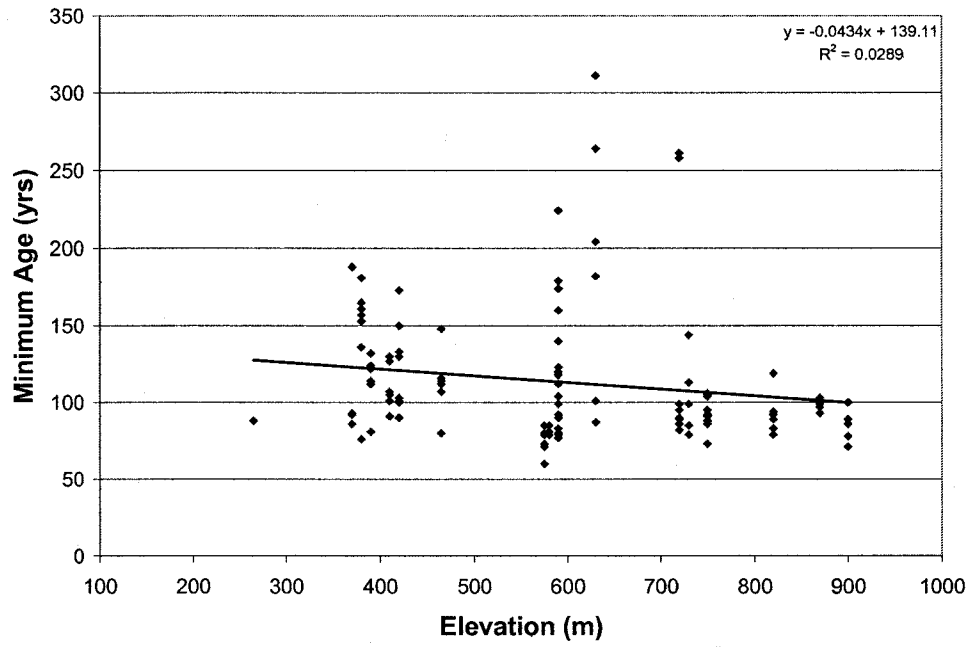


Figure 9a: Minimum age versus elevation, Schwarz field data collected from each of the 431 Valley-wide plots. The relationship between average minimum age and elevation decreases by 25.44 years between 300 and 900 m elevation. T-test p-value=0.0121, N=452. **9b**: 2005 re-sample, plot minimum age versus elevation. T-test p-value=0.0682, N=117. Each point represents the minimum age of a single tree within one of the Valley-wide plots resampled during the 2005 summer. This plot substantiates the Schwarz age and elevation trend with an average plot age decline of 26.04 years between 300 m and 900 m elevation.

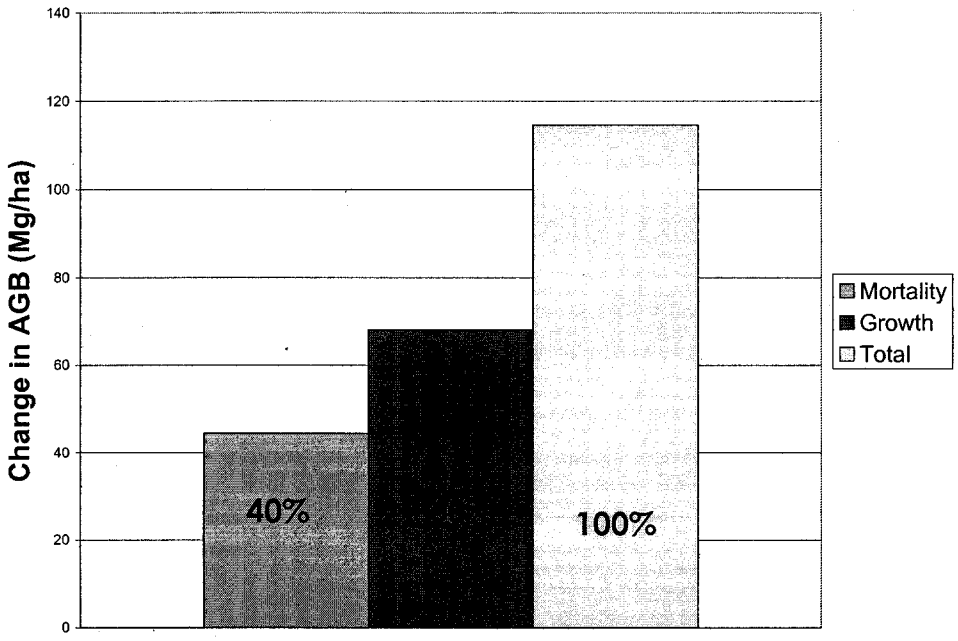
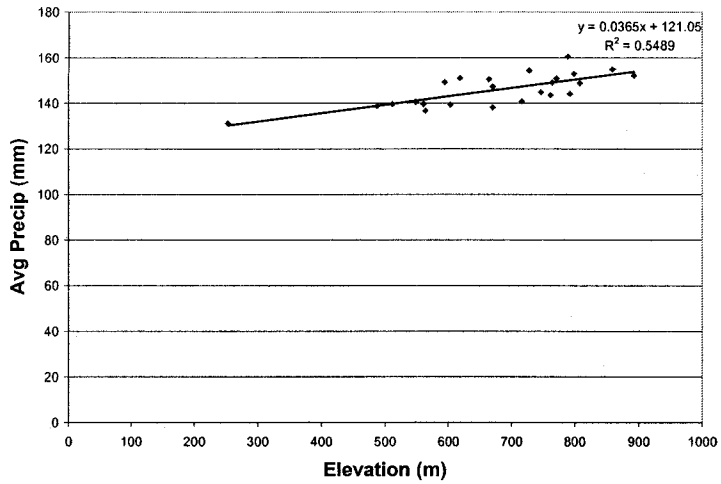
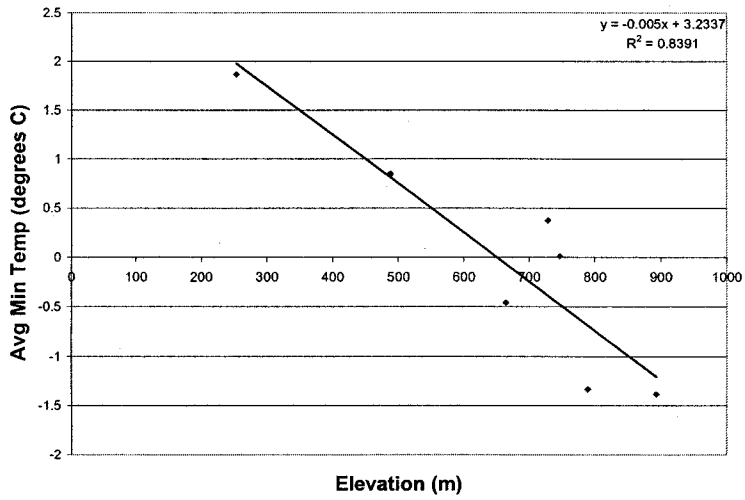


Figure 10: Relative importance of changes in net growth and mortality rates on change in AGB between 300 and 900 m elevation at Hubbard Brook.

a)



b)



c)

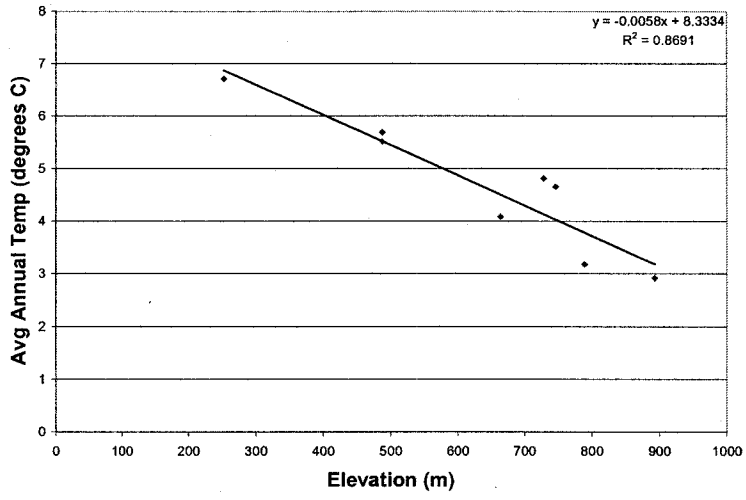
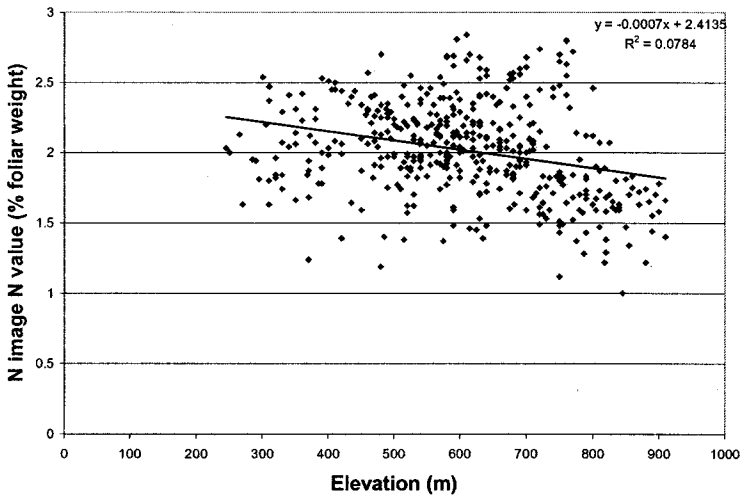


Figure 11a: Hubbard Brook meteorological data average precipitation versus elevation. T-test p-value<0.0001, N=24. **11b**: Hubbard Brook meteorological data average minimum temperature versus elevation. T-test p-value=0.0007, N=8. **11c**: Hubbard Brook meteorological data average annual temperature versus elevation. T-test p-value=0.0014, N=8.

a)

b)



c)

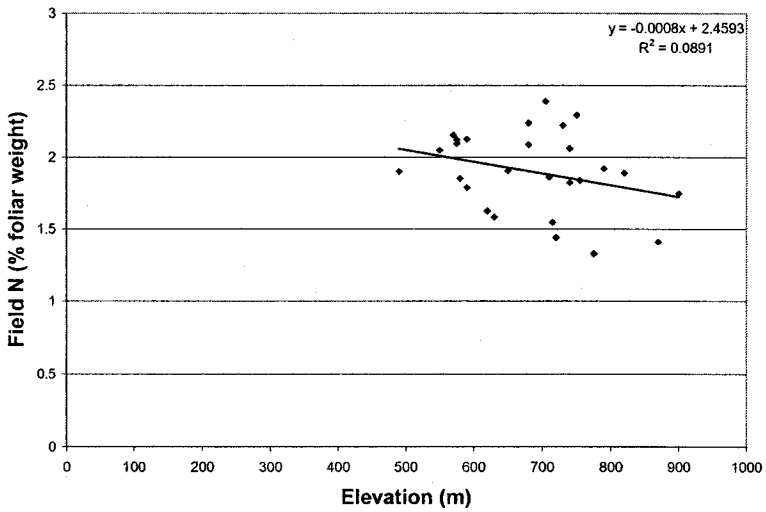
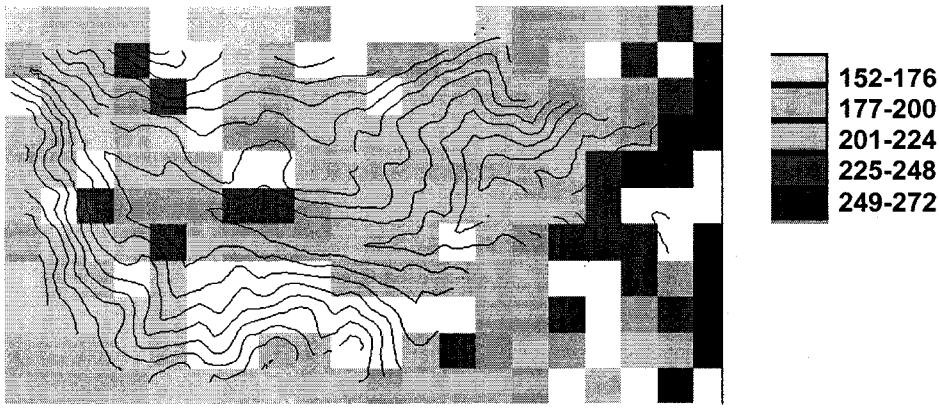
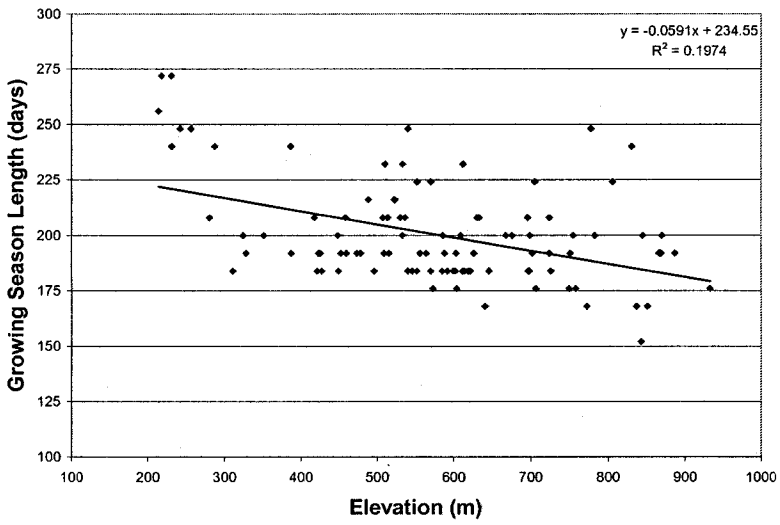


Figure 12a: Processed AVIRIS scene of Hubbard Brook and Valley plots. **12b**: AVIRIS image plot value N versus elevation. T-test p-value<0.0001, N=430. **12c**: Field Nitrogen versus elevation. T-test p-value=0.1173, N=26.

a)



b)



c)

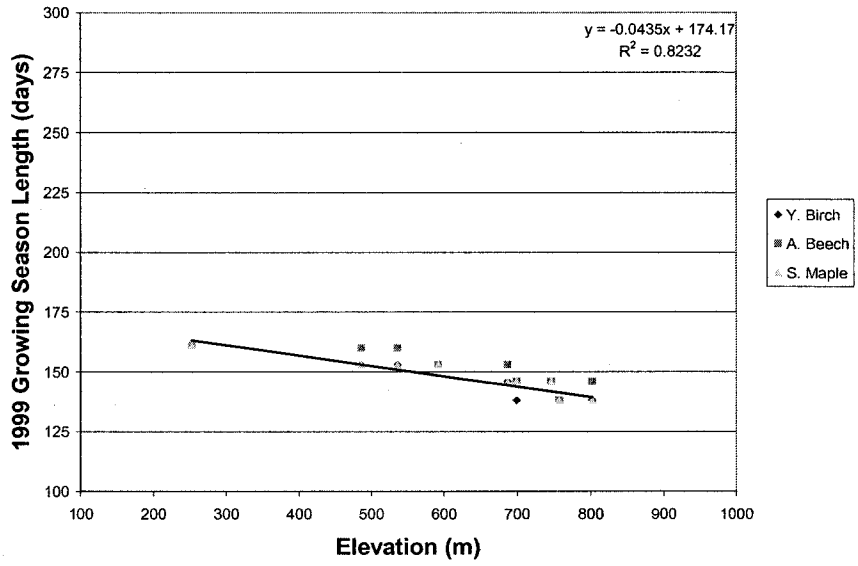
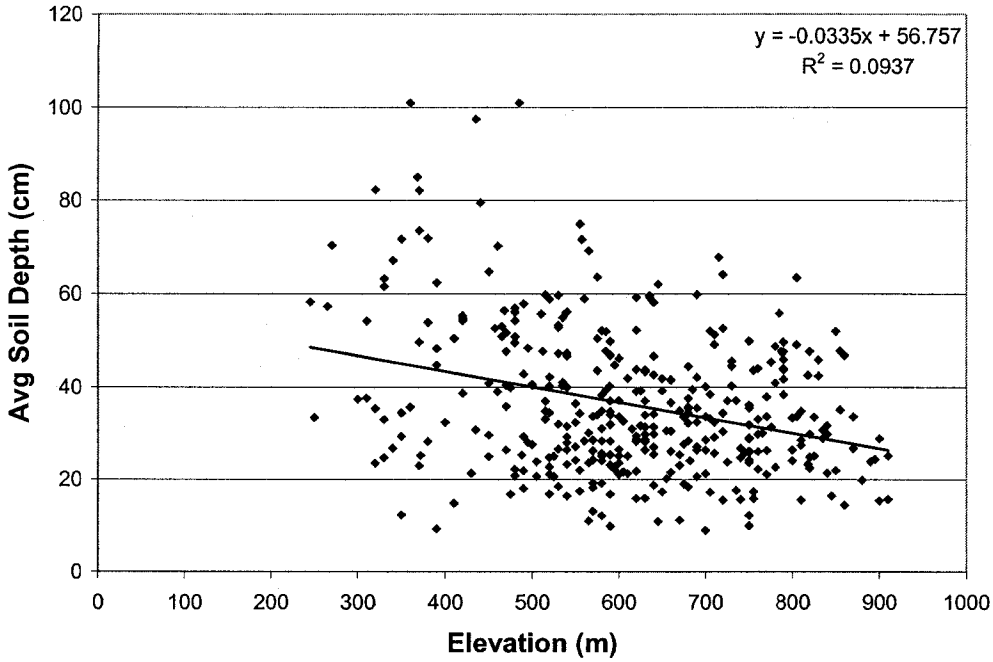


Figure 13a: Arcview image of MODIS derived growing season length overlaid with DEM elevation contours. White grid cells are no data. **13b:** 2002 MODIS derived growing season length versus elevation. MODIS growing season length shows the same 16% decline between 300 and 900 m elevation. T-test p-value<0.0001, N=101. **13c:** 1999 phenology data collected from 9 field sites at Hubbard Brook. Yellow birch, American beech, and Sugar maple trees monitored for leaf-on in the spring and leaf-off in the fall. Growing season length shows an average decrease of 16% between 300 and 900 m elevation. T-test p-

a)



b)

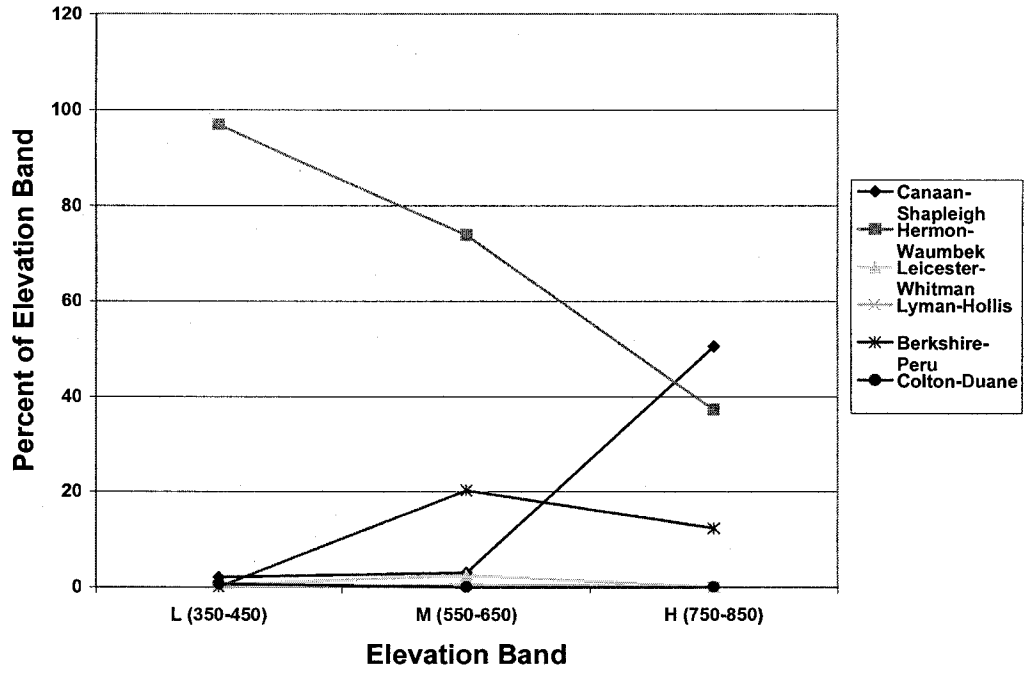
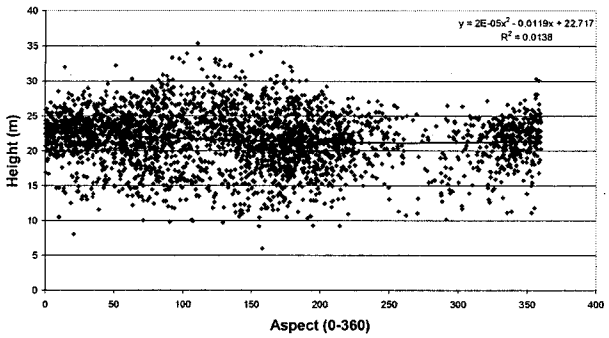
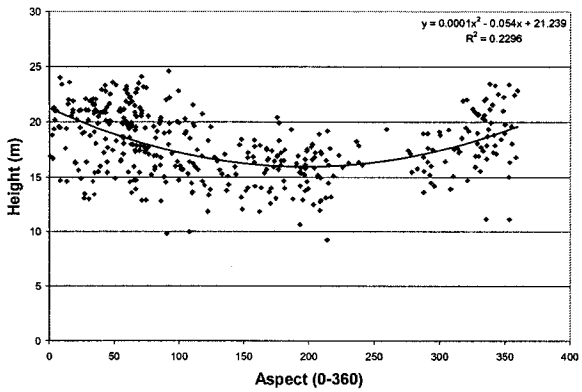


Figure 14a: Schwarz field data average plot soil depth versus elevation. T-test p-value<0.0001, N=432. **14b**: Hubbard Brook GIS data on soil type, grouped by elevation. At each elevational band (Low, Mid, and High), the area of each soil type is divided by the total area.

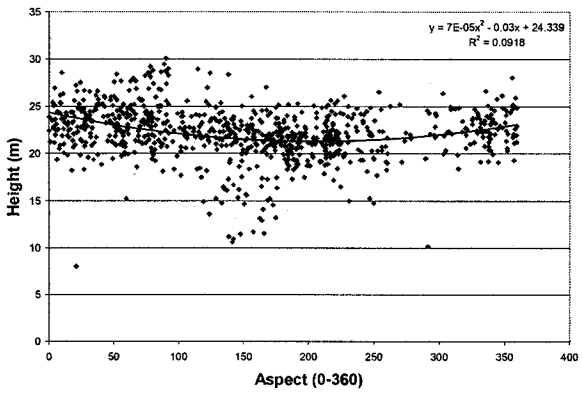
a)



b)



c)



d)

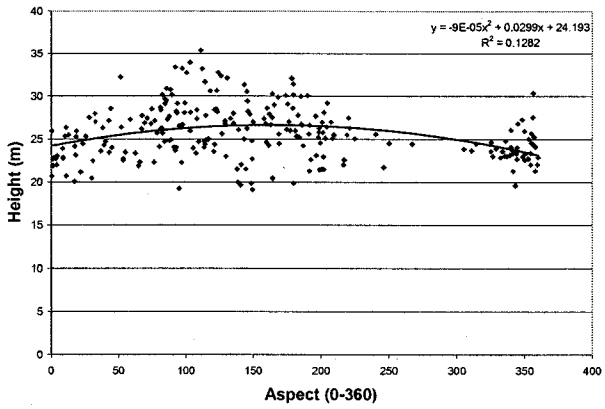


Figure 15a: LiDar analyses of canopy height versus aspect at all elevations. T-test p-value<0.0001, N=2958. **15b:** LiDar analyses of canopy height versus aspect at high elevations (750-850 meters). T-test p-value<0.0001, N=403. **15c:** LiDar analyses of canopy height versus aspect at mid elevations (550-650 meters). T-test p-value<0.0001, N=827. **15d:** LiDar analyses of canopy height versus aspect at low elevations (350-450 meters). T-test p-value=0.1943. N=403.

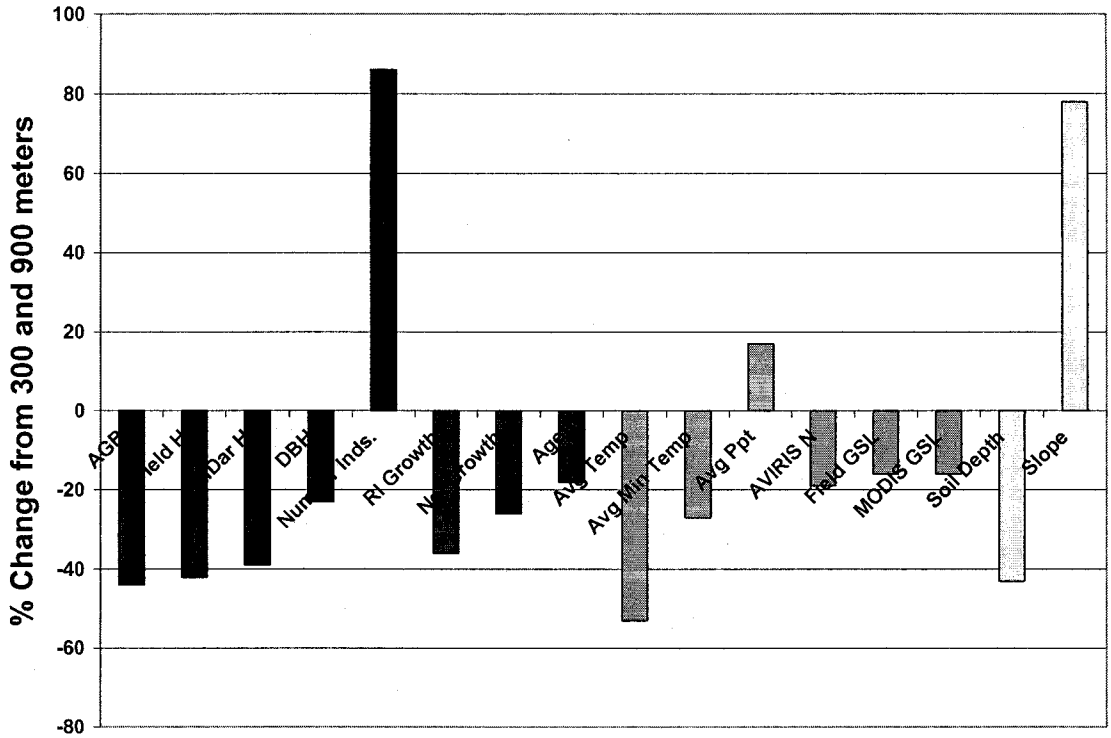


Figure 16: Percent change between 300 and 900 m elevation. First three bars represent the trends of interest: AGB, field measured height, and LiDar measured height. DBH and Number of Individuals (per plot) represent 'Ecosystem Structure' hypotheses. RI Growth, Net Growth, and Age are within our category of 'Growth and Mortality'. Average Temperature, Average Minimum Temperature, Average Precipitation, AVIRIS N, Field GSL (Growing Season Length), and MODIS GSL are all within our category of 'Direct Environmental Factors', and Soil Depth and Slope are within the 'Indirect Environmental Factors' category.

	Slope	Intercept	R^2	p-value
Soil Depth	0.54	183.8	0.02	0.0167
DBH	9.61	22.7	0.36	0.0001
Height	7.22	45.8	0.21	0.0001
No. Trees	-1.2	245.4	0.07	0.0001
RI Growth	42.22	111.7	0.27	0.0001
Net Growth	48.22	118.6	0.29	0.0001
AVIRIS N	68.26	66.8	0.11	0.0001

Figure 17: Regressions of environmental factors by AGB.

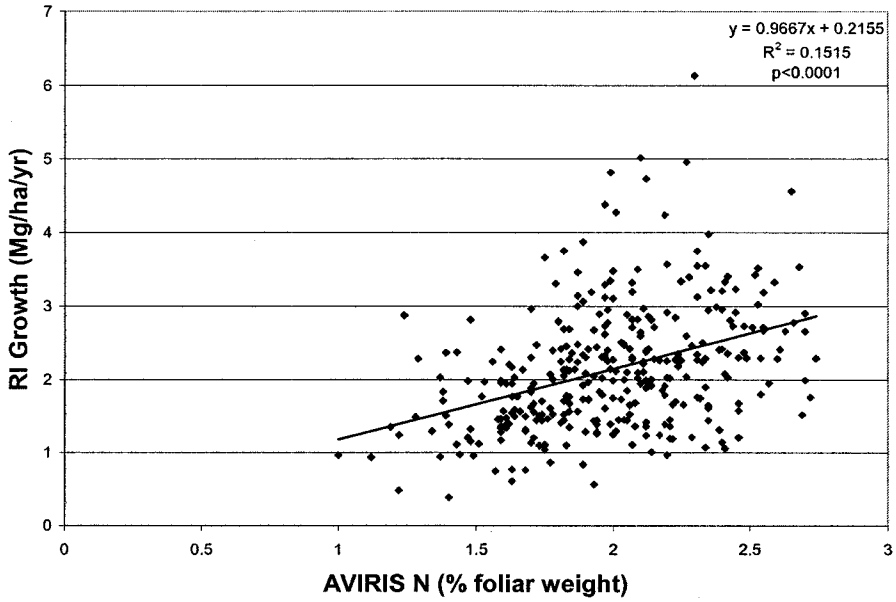


Figure 18: Radial increment growth estimate versus AVIRIS derived N concentration (% foliar weight). T-test p-value<0.0001, N=329.

LIST OF REFERENCES

Asrar, G., J. Kaye, and P. Morel. 2001. NASA Research Strategy for Earth System Science: Climate Component. American Meteorological Society.

Barrick, K., A. Schoettle. 1996. A comparison of the foliar nutrient status of elfinwood and symmetrically formed tall trees, Colorado Front Range, U.S.A. Canadian Journal of Botany 74: 1461-1475.

Becker, P., F. Meinzer, and S. Wullschleger. 2000. Hydraulic limitation of tree height: a critique. Functional Ecology 14: 4-11.

Bernhardt, E., G. Likens, D. Buso, and C. Driscoll. 2003. In-stream uptake dampens effects of major forest disturbance on watershed nitrogen export. PNAS 100(18): 10304-10308.

Bormann, B., and R. Sidle. 1990. Changes in productivity and distribution of nutrients in a chronosequence at Glacier Bay National Park, Alaska. The Journal of Ecology 78: 561-578.

Bohrmann, F., T. Siccama, G. Likens, and R. Whittaker. 1970. The Hubbard Brook Ecosystem Study: composition and dynamics of the tree stratum. Ecological Monographs 40(4): 373-388.

Brown, S. and P. Schroeder. 1999. Spatial patterns of aboveground production and mortality of woody biomass for Eastern U.S. forest. Ecological Applications 9(3): 968-980.

Clark, D., S. Brown, D. Kicklighter, J. Chambers, J. Thomlinson, and J. Ni. 2001. Measuring net primary production in forests: concepts and field methods. Ecological Applications 11(2): 356-370.

Cordell, S., G. Goldstein, F. Meinzer, and L. Handley. 1999. Allocation of nitrogen and carbon in leaves of Metrosideros polymorpha regulates carboxylation capacity and $\delta^{13}C$ along an altitudinal gradient. Functional Ecology 13: 811-818.

Ehleringer, J. and J. Vogel. 1993. Historical aspects of stable isotopes in plant carbon andwater relations, in Ehleringer, J., Hall, A. and Farquhar, G. (Eds), Stable Isotopes and Plant Carbon-Water Relations, Academic Press, Inc., San Diego, CA.

Fahey, T., T. Siccama, C. Driscoll, G. Likens, J. Campbell, C. Johnson, J. Battles, J. Aber, J. Cole, M. Fisk, P. Groffman, S. Hamburg, R. Holmes, P. Schwarz, and R.

Yanai. 2005. The biogeochemistry of carbon at Hubbard Brook. Biogeochemistry 75: 109-176.

Foster, J. and W. Reiners. 1983. Vegetation patterns in a virgin subalpine forest at Crawford Notch, White Mountains, New Hampshire. Bulletin of the Torrey Botanical Club 110(2): 141-153.

Gale N., and P. Hall. 2001. Factors determining the modes of tree death in three Bornean rain forests. Journal of Vegetation Science. 12 (3): 337-346.

Goetz, A., B. Rock, and L. Rowan. 1983. Remote sensing for exploration: an overview. Economic Geology 78(4): 573-590.

Hadley, J. and W. Smith. 1986. Wind effects on needles of timberline conifers: seasonal influence on mortality. Ecology 67(1): 12-19.

Hansen-Bristow, K. 1986. Influence of increasing elevation on growth characteristics at timberline. Canadian Journal of Botany 64: 2517-2523.

Hurtt, G., R. Dubayah, J. Drake, P. Moorcroft, S. Pacala, J. Blair, and M. Fearon. 2004. Beyond potential vegetation: combining LiDar data and a height-structured model for carbon studies. Ecological Applications 14(3): 873-883.

Hurtt, G., S. Pacala, P. Moorcroft, J. Caspersen, E. Shevliakova, R. Houghton, and B. Moore. 2002. Projecting the future of the U.S. Carbon sink. Proceedings of the National Academy of Sciences 99(3): 1389-1394.

IGBP Annual Report 2003. IGBP Secretariat. Editor: B. Young.

IPCC Third Assessment Report: Climate Change 2001. Editor: R. Watson.

Jobbagy, E., and R. Jackson. 2000. Global controls of forest line elevation in the northern and southern hemispheres. Global Ecology and Biogeography 9(3): 253-268.

Jonsson, P. and L. Eklundh. 2004. TIMESAT—a program for analyzing time-series of satellite sensor data. Computers and Geosciences 30: 833-845.

Jonsson, P. and L. Eklundh. 2006. TIMESAT—a program for analyzing time-series of satellite sensor data. Users Guide for TIMESAT 2.2.

Joshi, A., D. Vann, A. Johnson, and E. Miller. 2003. Nitrogen availability and forest productivity along a climosequence on Whiteface Mountain, New York. Canadian Journal of Forest Research 33: 1880-1891.

Kitayama, K., and S. Aiba. 2002. Ecosystem structure and productivity of tropical rain forests along altitudinal gradients with contrasting soil phosphorus pools on Mount Kinabalu, Boreo. Journal of Ecology 90: 37-51.

Korner, C. 1999. Alpine Plant Life. Springer-Verlag, Berlin.

Korner, C., G. Farquhar, and Z. Roksandic. 1988. A global survey of carbon isotope discrimination in plants from high altitude. Oecologia 74: 623-632.

Lefsky, M., D. Turner, M. Guzy, and W. Cohen. 2005. Combining Lidar estimates of aboveground biomass and Landsat estimates of stand age for spatially extensive validation of modeled forest productivity. Remote Sensing of Environment 95: 549-558.

Likens, G., C. Driscoll, D. Buso, T. Siccama, C. Johnson, D. Ryan, G. Lovett, T. Fahey, and W. Reiners. 1994. The biogeochemistry of potassium at Hubbard Brook. Biogeochemistry 25:61-125.

Likens, G., C. Driscoll, D. Buso, T. Siccama, C. Johnson, G. Lovett, T. Fahey, W. Reiners, D. Ryan, C. Martin, and S. Bailey. 1998. The biogeochemistry of calcium at Hubbard Brook. Biogeochemistry 41(2): 89-173.

Meinzer, F., G. Goldstein, and P. Rundel. 1984. Morphological changes along an altitude gradient and their consequences fir an Andean giant rosette plant. Oecologia 65(2): 278-283.

Merrens, E., and D. Peart. 1992. Effects of hurricane damage on individual growth and stand structure in a hardwood forest in New Hampshire, USA. Journal of Ecology 80(4): 787-795.

Moorcroft, P., G. Hurtt, and S. Pacala. 2001. A method for scaling vegetation dynamics: the Ecosystem Demography Model (ED). Ecological Monographs 71(4): 557-586.

Oleksyn, J., J. Modrzynski, M. Tjoelker, R. Zytkowiak, P. Reich, and P. Karolewski. 1998. Growth and physiology of *Picea abies* populations from elevational transects: common garden evidence for altitudinal ecotypes and cold adaptation. Functional Ecology 12: 573-590.

Oleksyn, J., P. Reich, R. Zytkowiak, P. Karolewski, and M. Tjoelker. 2002. Needle nutrients in geographically diverse *Pinus sylvestris* populations. Annals of Forest Science 59: 1-18.

Ollinger, S. and M. Smith. 2005. Net primary productivity and canopy nitrogen in a temperate forest landscape: an analysis using imaging spectroscopy, modeling and field data. Ecosystems 8: 760-778.

Peart, D., C. Cogbill, and P. Palmiotto. 1992. Effects of logging history and hurricane damage on canopy structure in a northern hardwoods forest. Bulletin of the Torrey Botanical Club 119(1): 29-38.

Pederson, B. 1998. The role of stress in the mortality of Midwestern oaks as indicated by growth prior to death. Ecology 79(1): 79-93.

Phillips, N., B. Bond, N. McDowell, M. Ryan, and A. Schauer. 2003. Leaf area compounds height-related hydraulic costs of water transport in Oregon white oak trees. Functional Ecology 17: 832–840.

Raich, J., A. Russell, and P. Vitousek. 1997. Primary productivity and ecosystem development along an elevational gradient on Mauna Loa, Hawai'i. Ecology 78(3): 707-721.

Reiners, W., D. Hollinger, and G. Lang. 1984. Temperature and evapotranspiration gradients of the White Mountains, New Hampshire, U.S.A. Arctic and Alpine Research 16(1): 31-36.

Rhoads, A., S. Hamburg, T. Fahey, T. Siccama, E. Hane, J. Battles, C. Cogbill, J. Randall, and G. Wilson. 2002. Effects of an intense ice storm on the structure of a northern hardwood forest. Canadian Journal of Forest Research 32: 1763-1775.

Richardson, A. 2004. Foliar Chemistry of balsam fir and red spruce in relation to elevation and the canopy light gradient in the mountains of northeastern United States. Plant and Soil 260: 291-299.

Richardson, A. and G. Berlyn. 2002. Spectral Reflectance and photosynthetic properties of Betula papyrifera leaves along an elevational gradient on Mt. Mansfield, Vermont, USA. American Journal of Botany 89(1): 88-94.

Richardson, A., G. Berlyn, and S. Duigan. 2003. Reflectance of Alaskan black spruce and white spruce foliage in relation to elevation and latitude. Tree Physiology 23: 537-544.

Richardson, A., X. Lee, and A. Friedland. 2004. Microclimatology of treeline spruce–fir forests in mountains of the northeastern United States. Agricultural and Forest Meteorology 125: 53–66.

Rock, B., J. Vogelmann, D. Williams, A. Vogelmann, and T. Hoshizaki. 1986. Remote detection of forest damage. Bioscience 36(7): 439-445.

Sabo, S. 1980. Niche and habitat relations in subalpine bird communities of the White Mountains of New Hampshire. Ecological Monographs 50: 241–259.

Salter, R. 1940. Some soil factors affecting tree growth. Science 91(2365): 391-398.

Schoettle, A. 1990. The interaction between leaf longevity and shoot growth and foliar biomass per shoot in Pinus contorta at two elevations. Tree Physiology 7: 209 214.

Schwarz, P., T. Fahey, C. Martin, T. Siccama, and A. Bailey. 2001. Structure and composition of three northern hardwood-conifer forests with differing disturbance histories. Forest Ecology and Management 144: 201-212.

Schwarz, P., T. Fahey, and C. McCullough. 2003. Factors controlling spatial variation of tree species in a forested landscape. Ecology 84(7): 1862-1878.

Siccama, T., S. Hamburg, M. Arthur, R. Yanai, F. Bormann, and G. Likens. 1994. Corrections to allometric equations and plant tissue chemistry for Hubbard Brook Experimental Forest. Ecology 75(1): 246-248.

Singh, S., B. Adhikari, and D. Zobel. 1994. Biomass, productivity, leaf longevity, and forest structure in the central Himalaya. Ecological Monographs 64(4): 401-421.

Smith, M., S. Ollinger, M. Martin, J. Aber, R. Hallett, and C. Goodale. 2002. Direct estimation of aboveground forest productivity through hyperspectral remote sensing of canopy nitrogen. Ecological Applications 12(5): 1286-1302.

Smith, M., M. Martin, S. Ollinger and L. Plourde. 2003. Analysis of hyperspectral data for estimation of temperate forest canopy nitrogen concentration: comparison between an airborne (AVIRIS) and a spaceborne (HYPERION) sensor. IEEE Transactions on Geoscience and Remote Sensing, 41(6): 1332 - 1337.

Sollins, P. 1998. Factors influencing species composition in tropical lowland rain forest: does soil matter? Ecology 79(1): 23-30.

Sparks, J. and J. Ehleringer. 1997. Leaf carbon isotope discrimination and nitrogen content for riparian trees along elevational transects. Oecologia 109: 362-367.

Taiz, L. E. Zeiger. 1998. Plant Physiology, Third Edition. Sinauer Associates.

Turner, D. P., S. V. Ollinger, M. L. Smith, O. Krankina and M. Gregory. 2004. Scaling net primary production to a MODIS footprint in support of Earth Observing System product validation. International Journal of Remote Sensing, 25(10): 1961 - 1980.

Van de Water, P., S. Leavitt, and J. Betancourt. 2002. Leaf $\delta^{13}C$ variability with elevation slope aspect, and precipitation. Oecologia 132: 332-343.

Vitouesk, P., C. Field, P. Matson. 1990. Variation in foliar $\delta^{13}C$ in Hawaiian *Metrosideros polymorpha*: a case of internal resistance? Oecologia 84: 362-370.

Waide, R., J. Zimmerman, and F. Scatena. 1998. Controls of primary productivity: lessons from the Luquillo Mountains in Puerto Rico. Ecology 79(1): 31-37.

Wardle, P. 1968. Engelmann spruce at its upper limits on the Front Range, Colorado. Ecology 49(3): 483-495.

Weathers, K., G. Lovett, G. Likens, and R. Lathrop. 2000. The effect of landscape features on deposition to Hunter Mountain, Catskill Mountains, New York. Ecological Applications 10(2): 528-540.

Weaver, P. 1990. Forest structure and productivity in Puerto Rico's Luquillo Mountains. Biotropica 22(1): 69-82.

Whittaker, R., F. Bohrmann, G. Likens, T. Siccama. 1974. The Hubbard Brook Ecosystem Study: forest biomass and production. Ecological Monographs 44(2): 233-254.

Whittaker, R. and W. Niering. 1975. Vegetation of the Santa Catalina Mountains Arizona v. biomass production and diversity along the elevation gradient. Ecology 56: 771-790.

Zhang, X., M. Friedl, C. Schaaf, and A. Strahler. 2004. Climate controls on vegetation patterns in northern mid- and high latitudes inferred from MODIS data. Global Change Biology 10: 1133-1145.

Zhang, X., M. Friedl, C. Schaaf, and A. Strahler. 2005. Monitoring the response of vegetation phenology to precipitation in Africa by coupling MODIS and TRMM instruments. Journal of Geophysical Research 110: D12103.

APPENDICES

APPENDIX A

Hydraulics and Height Limitation

Phillips et al. (2003) assessed the relationship between leaf area and height-related hydraulic costs of water transport. Their experiment involved *Quercus garryana* trees which is a species that exhibits an increased leaf to sapwood area ratio with increased tree size. Phillips et al. (2003) found that 25 m *Q. garryana* had lowered water flux and carbon isotope discrimination compared to 10 m trees. Whole tree water fluxes were smaller in 25 m trees in per unit sapwood and especially per leaf area. The increase in leaf area to sapwood area ratio with tree size contradicts what is expected if this ratio is regulated to maintain leaf gas exchange. The observed changes in leaf area to sapwood area ratio within this study serve to worsen, not better, differences in leaf gas exchange. Substantial differences in leaf specific hydraulic conductance also support the theory of size related hydraulic limitation to canopy gas exchange and net carbon gain. Also, leaf carbon isotope discriminations suggest reductions in stomatal conductance in 25 m compared with 10 m *Q. garryana*.

The linkage between hydraulic and gas exchange variables measured in this study is well explained by the hydraulic limitation hypothesis. Phillips et al. (2003) note that drought-

adapted species such as *Q. garryana* can provide a challenging test to the hydraulic limitation hypothesis because drought and tree height are the basis of very similar impediments to tree function. Both drought and tree height reduce leaf and xylem water potentials, thus affecting photosynthetic function and vulnerability to xylem cavitation. In their critique of hydraulic limitation on tree height, Becker et al. (2000) stress the importance of taking a whole-plant perspective in the analysis of tree height limitation. This involves the incorporation of soil and atmospheric factors in analysis of tree height limits. Ground measurements must be made to understand the relationship of tree height to growth at different elevations

APPENDIX B

Isotope Analysis of Drought Stress

The carbon-13:carbon-12 isotope ratio is an indicator of plant stomatal conductance. Plants preferentially utilize the lighter form (carbon-12) rather than the heavier form of carbon, carbon-13. However, when a plant's stomata are closed, the supply of carbon dioxide becomes limited and the plant is forced to utilize any unused carbon-13 that may remain in intercellular air spaces. Since drought stressed plants typically increase stomatal closure to reduce water loss, they tend to have a lower carbon-13:carbon-12 isotope ratio because they are using more carbon-13 than a non-drought stressed plant would. For these reasons, the foliar ratio of carbon-13:carbon-12 isotope has been used to identify changing environmental conditions along an elevational gradient (Van de Water et al. 2002).

The efficiency by which plants balance their need for carbon and reduce water loss through gas exchange can be analyzed by comparing the carbon-13 to carbon-12 ratio between plants. In C_3 plants, the $\delta^{13}C_{leaf}$ is a result of enzymatic fractionation through stomatal and mesophyll resistance to diffusion of carbon dioxide. (Ehleringer and Vogel 1993) This fractionation can be represented by the following equation:

$$\delta^{13}C_{leaf} = \delta^{13}C_{air} - a(b-a)C_i / C_a$$

(a equals 4.4‰, b is the combination of RuBp and PEP carboxylase which equals 27‰, and C_i / C_a is the ratio of internal to atmospheric carbon dioxide.)
(Ehleringer and Cerling 1995)

Leaf carbon isotope analysis typically demonstrates an increase in carbon-13 at higher elevation sites (Korner et al. 1988, 1991, and Sparks and Ehrlinger 1997). This increase in carbon-13 isotope concentrations relates to physiological changes in leaf thickness, leaf nitrogen content, and stomatal conductance and density. Changes in carbon-13 concentrations relate to environmental changes in soil moisture, air temperature, and partial pressures of oxygen and carbon in the atmosphere. Higher temperatures tend decrease availability of soil moisture at lower elevations and south facing slopes. Van de Water et al. tested four hypotheses in their 2002 paper: first, that drought stress leads to changes in $\delta^{13}C_{leaf}$ values with elevation, slope, aspect, and latitude; second, $\delta^{13}C_{leaf}$ differences with elevation and slope aspects among taxonomic and functional groups are consistent between two transects; third, any differences between the two transects for same species is attributed to differences in amount of precipitation; and fourth, C_4 plants are insensitive to changing conditions and demonstrate relatively stable $\delta^{13}C_{leaf}$ values across changing environmental conditions.

Van de Water et al. (2002) sampled plants along elevational gradients on north and south facing slopes in Utah and New Mexico. The 1,525 to 1,675 m gradients covered the transition zone between desert scrub to mixed conifer forest. At each site, the photosynthetic tissue of five plants of each species were sampled. Results showed that

$\delta^{13}C_{leaf}$ values at lower elevations increased in C_3 plants as expected. The less negative $\delta^{13}C_{leaf}$ values at lower elevation sites suggests that physiological and morphological changes with increasing elevation are secondary to the physiological effect of restricted water availability at lower elevations. (Van de Water et al. 2002) significant differences between species occurred only within gymnosperms. C_3 angiosperms were significantly depleted in $\delta^{13}C_{leaf}$ compared to co-occurring gymnosperms. Results from this study also showed that changes in $\delta^{13}C_{leaf}$ are associated not only with changes in elevation, precipitation, and aspect, but also in soil type. Change in soil types may mark the point at which drought stress overcomes any impact of other biotic or abiotic factor on the $\delta^{13}C_{leaf}$ value.

Analysis of $\delta^{13}C_{leaf}$ may help researchers to better understand physiological changes occurring within a plant and map these changes with associated changes in environmental factors. By isolating factors that impact $\delta^{13}C_{leaf}$ values, it may be possible for researchers to better understand what important factors limit tree growth with changes in elevation.

APPENDIX C

Applicability of Hyperspectral Remote Sensing

Hyperspectral Remote Sensing may be utilized to spatially map changes in environmental factors that have a direct impact on changes in AGB and tree height with elevation at Hubbard Brook. Hyperspectral methods have been established to estimate foliar nitrogen concentration and aboveground forest productivity (Smith et al. 2000, Smith et al. 2003). Hyperspectral remote sensing may provide an opportunity for more accurate interpretation of field and LiDar data at Hubbard Brook and extrapolation to larger spatial scales. Remote sensing has a wide range of uses in the study of forest ecosystems (Goetz et al. 1983). Hyperspectral remote sensing presents data in spectral ranges far beyond visible light. The hyperspectral reflectance curve of vegetation can provide information on leaf pigments, cell structure, and leaf water content. Chlorophyll strongly absorbs visible light (from 0.4 to 0.7 μm) for use in photosynthesis. The cell structure of the leaves, on the other hand, strongly reflects near-infrared light (from 0.7 to 1.1 μm). The more leaves a plant has, the more these wavelengths of light are affected, respectively. A typical reflectance curve for a healthy photosynthetic plant demonstrates strong absorption features at 0.480 and 0.680 μm as a result of high chlorophyll concentrations in the leaf. Spectral curves show subtle changes that occur during the growing season

such as buildup of tannins within the leaves. Smith et al. (2000) demonstrated direct estimation of aboveground forest productivity through hyperspectral remote sensing of canopy nitrogen within the 360,000 hectare White Mountain National Forest. Plant responses to environmental conditions may have spectral "signatures" that can enable managers to identify and monitor forest health (Rock et al. 1986). Studies such as these emphasize the value of hyperspectral remote sensing in determining landscape level dynamics accurately. Richardson and Berlyn (2002) specifically analyzed the spectral reflectance and photosynthetic properties of mountain paper birch along an elevational gradient on Mt. Mansfield in Vermont. They noted trends such as decreasing photosynthesis and lowered chlorophyll content as elevation increased. Leaf reflectance has been identified as an important indicator of stress in black and white spruce along an elevational gradient in Alaska (Richardson et al. 2003).